THE BREEDING SYSTEM OF THE SOUTH ISLAND RIFLEMAN (*ACANTHISITTA CHLORIS*) AT KOWHAI BUSH, KAIKOURA, NEW ZEALAND.

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Gregory H. Sherley

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ABSTRACT

Two populations of Riflemen (Acanthisitta chloris chloris) at Kowhai Bush, Kaikoura on the east coast of the South Island of New Zealand, were studied for four and three years. It was predicted that because Riflemen were exceptionally small and potentially energetically constrained they would employ a highly cooperative parental care system. Riflemen parents displayed a high degree of cooperation throughout the breeding cycle.

Parental effort was measured throughout the breeding cycle which entailed rearing two broods. Prior to and during laying first clutches the male fed the female and it was estimated that courtship-feeding supplied the female with the extra food required for oogenesis. Incubation was shared with the male sitting for about half as long again as the female during the day and the female only sitting during the night.

Male parents fed offspring about one and a half times as often as females did. Sometimes parents benefitted from helpers feeding their offspring with the male parents benefitting the most. Occasionally helpers benefitted by acquiring mates from the brood they helped.

In other forms of parental care there was a high degree of parental cooperation with males undertaking most of the nest-building and about an equal share in territorial defence.

Riflemen are sexually dimorphic with females about 0.25 times larger than males. The reason for the difference in size was discussed and the relationship between parental investment, sexual dimorphism and sex ratio was investigated with respect to Fisherian theory. It was concluded that females were more costly to rear but, because Riflemen were rearing smaller broods than was theoretically possible, they were left with enough latitude to rear a larger sex without a primary sex ratio adjustment.

INTRODUCTION

"Behavioural ecology is the second major root of ecological energetics [environmental physiology the first] and it is clear that knowledge of behavioural phenomena is critical to a comprehension of the energetic constraints acting upon animals."

Glen Walsberg (1983)

1. Taxonomy and previous research

The South Island Rifleman (*Acanthisitta chloris chloris*) is one of the smallest passerines in the world. It is possibly one of the most successful of New Zealand's endemic birds, as it has resisted extinction, exploited man-modified habitats (Williams 1973) and survived the introductions of mammalian predators. The Riflemen's survival and exploitation of man modified habitats has not been paralleled by another New Zealand species which is endemic at the Family level. Instead much of New Zealands' avifauna has become extinct since man colonised New Zealand, including three of the Rifleman's confamilials. The other confamilial (the Rockwren *Xenicus gilviventris*) surviving has suffered extensive reduction in distribution and is currently considered endangered.

The Rifleman is a sexually dimorphic, invertebrate eating, hole nesting forest dweller weighing 5 - 8g. Research on Riflemen started with Gray's (1969) study, which identified a protracted breeding cycle and territorial behaviour as two main characteristics of breeding. B.M. Fitzgerald and P.D. Gaze (pers comm) have studied the breeding success and nestling growth rate of the North Island subspecies (*A . c . granti*) and found that female Riflemen are larger than males. Riflemens' reversed from usual sexual dimorphism has been investigated in the present study.

The taxonomic position of Riflemen has been unclear for some time (Sibley et. al. 1982). Recently, however, Sibley et al determined with DNA-DNA hybridization that the Family to which Riflemen belong (Acanthisittadae) is a member of the suboscine suborder Oligomyodi. Sibley et al also concluded that Riflemen were so unlike other suboscine passerines as to warrant placing them in their own Infraorder, Acanthisittides. This lack of similarity to living species suggests that Riflemen probably branched from other passerine stock during the Cretaceous, when New Zealand separated from Gondwanaland (Fleming 1979).

2.The problem of small size

Equations relating thermal conductance and size indicate that at low temperatures smaller birds lose heat at a faster rate than large birds do (Ricklefs 1974). Kendeigh et. al. (1977) stated (page 145) "that a decrease in size brings an increase in energy stress" and postulated that the lower limit of size for a bird is constrained by an ability to maintain a metabolic rate of between 2.2 and 2.5 kcal/g/day over an extended period. Further, birds in temperate zones can tolerate a drop in ambient temperature to only about 0°C and at this temperature, the energy required to stay alive ("existence metabolism") is maximum. Riflemen experience temperatures below 0°C during winter and early in the breeding season (see appendix 4).

Productive energy is thought to be the difference between available energy and energy required for existence. The remainder is the energy available for activities such as reproduction, and is a function of temperature and metabolism which are in turn functions of body size (Kendeigh et. al. 1977). Under Kendeigh's model, as animals become smaller and ambient temperatures become lower, less energy is available to

the bird for extra demands such as reproduction.

A factor which influences the efficient use of a bird's time and energy resources is the high rate of power consumption by birds compared to their capacity to store energy (Walsberg 1983). The time span over which a small passerine can store sufficient food for maintenance is in the order of one or two days, hence the bulk of energy required for reproduction must be drawn from day to day food availability.

Physiological variables such as respiration frequency and heart beat frequency both increase dramatically with decreasing body weight under 100g according to Calder's (1974) graphs (his Figure 2). Non-linear relationships exist between body weight and metabolism which reveal that at the smallest sizes metabolic rates are maximum, yet a small animal must still retain minimum efficiency ratios such as the ratio of work output to energy intake. The difficulty in maintaining optimum efficiency ratios was evidenced in Gibb's (1954) observation that the proportion of time spent feeding was inversely related to body size for a number of small passerine species (body size range of 5-18g feeding rate = $kM^{-0.28}$). One interpretation of these results suggested by Calder was that the physiological lifespan of smaller birds is shorter than that of larger birds. This constraint on life span and, concommitantly, reproductive opportunities, could have a significant influence on the parental investment strategy of a species.

Considering the above implications of small body size for the Rifleman, their organisation of parental effort during the breeding period should be a result of maximising energetic efficiency.

3. Riflemen as a test case

The successful passerine radiation into different niches has been attributed to their acquiring small body size (Ralls 1977). The theoretical hypothesis addressed in this thesis is that Riflemen are at or near the limit of small size that is sustainable for a Passeriforme in New Zealand's latitudes, and that small body size imposes physical and energetic constraints on reproductive behaviour.

Walsberg (1983) pointed out that the reproductive cycle is energetically discrete from other phases of the annual cycle and therefore offers an excellent ecological unit for study. For this reason the present study uses the Rifleman breeding cycle as a convenient interval over which to investigate the size constraint hypothesis.

Case (1978) (page 869) has argued that "among extant animals each species' reproductive features are shaped more by attributes of its niche and habitat than by its body size." It is outside the scope of this study to test the relative importance of endothermy, altriciality, feeding ecology, habitat and environmental variables such as temperature or their inter-relationships (including their historical order of importance) as they influence behaviour within or between the breeding and nonbreeding periods. In the present author's view these factors all significantly influence behaviour for any highly altricial, endothermic animal such as Riflemen, but are most acute for an animal of exceptionally small size living in a low latitude country such as Riflemen in New Zealand.

Hopson (1973) postulated that parental care and altriciality were a consequence of selection for endothermy and small body size. Case (1978) (page 868) agreed with Hopson that "small size and endothermy were essential ingredients historically for the initial refinement and radiation of extended postnatal parental care." This thesis tests a refinement of

Case's hypothesis by postulating that because of the Riflemen's exceptionally small size and apparent success "extended parental care" will include a considerably high degree of parental cooperation.

4. Questions and predictions addressed

A. General

(i) Parental cooperation results in high male parental effort. The prediction is tested in the thesis by measuring male and female parental work at all stages in the breeding cycle and the timing of various parental responsibilities.

(ii) The Rifleman breeding cycle is protracted relative to other passerines.

B. Parental cooperativity

(i) Courtship-feeding: Does courtship-feeding constitute a significant male investment and is courtship-feeding important to the female?

(ii) Does incubation theoretically constitute a net loss of energy in an individual's energy budget? Which parent is most advantaged during incubation?

(iii) Nestling and post-fledging periods are the most energetically expensive form of parental effort and therefore a high degree of parental cooperation was predicted at these stages.

(iv) Other forms of parental effort include nest building and territorial defence. It was predicted that the male would undertake most work defending territory as suggested by Gray's (1974) study and that the male would make an important contribution in nest-building.

(v) The timing of moulting was investigated in relation to the rest of the breeding cycle.

(vi) Given that parental care for two broods overlapped, was the male's behaviour consistent with parents employing a cooperative breeding system?

C. Non-parental cooperation

(i) What advantages are there to the parents, offspring and helpers in helping?

D. Sexual dimorphism, sex ratio, offspring survival and parental investment

(i) Fisher (1958) predicted that if one sex costs parents more to raise than the other, there will be an adustment in primary sex ratio in favour of the least expensive sex. This prediction was tested.

(ii) Why do Rifleman display reversed from normal sexual dimorphism?

E. Interspecific comparisons

(i) Riflemen are compared with other Kowhai Bush passerines especially Grey Warblers (Gerygone igata) as the latter are about the same size as Riflemen, and therefore serve as an "ecological foil" to Riflemen.

GENERAL METHODS

1. Study area

Kowhai Bush is at 42° 23' south and 173° 37' east situated in coastal Marlborough on the north east side of the South Island of New Zealand (see Illustration 1). On New Zealand mapping series #1 map S49 the grid reference of Kowhai Bush is 895 953.

The bush borders the northern bank of the Kowhai River and serves as a flood protection reserve administered by the Marlborough Catchment Board. It is accessible by road about 8km from the University of Canterbury Edward Percival Field Station which is situated in the Kaikoura township.

In the first breeding season (1980-81) the study area included the whole 240ha area of the reserve. The composition of vegetation in the various types of forest which have been identified is described in Hunt and Gill (1979). However, over the remaining three summers the research was carried out in the south eastern end of the bush south of Floodgate Creek (see Illustration 1) in an area of about 80 ha and a 6 ha offlying patch of bush surrounded by farm land.

(i) Vegetation. The forest where most of the study was undertaken was open and flat. The dominant species was Leptospermum ericoides F.Myrtaceae which ranged in height from 5-7m. These trees were well spaced and afforded easy access and excellent visibility.

The larger area which was adjacent to the rest of Kowhai Bush reserve is subsequently referred to as the main study area. This forest was essentially devoid of undergrowth over about one third of its area. Where undergrowth occurred it consisted mainly of exotic species especially the yellow flowering broom Cytisus monspessulanus . Some native undergrowth

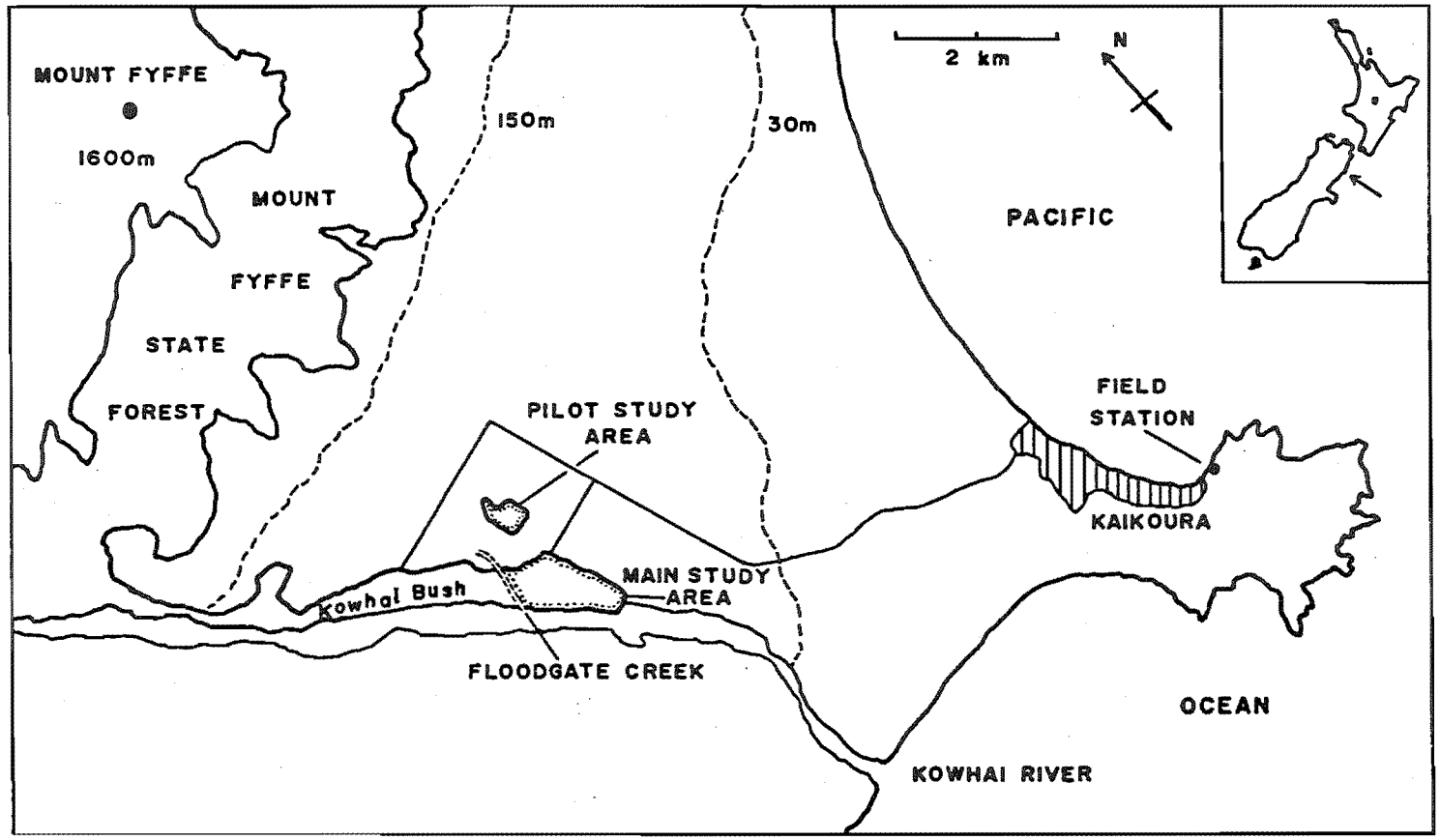


Illustration 1 Locality map of study areas.

species included Black Matipo *Pittosporum tenuifolium*, Tutu *Coraria arborea*, Mahoe *Melicytus ramiflorus* and *Coprosma lucida*.

The smaller study area was grazed (subsequently referred to as the pilot study area) and contained no undergrowth. The pilot study area was separated by a minimum of 100m of pasture from the main study area. The only species present was *L. ericoides* which was 3-6m in height.

(ii) Climate. Though the conditions of the Kaikoura area have been described by Gill (1980a) and Powlesland (1980) as "warm temperate" which is consistent with Hurnard's (1978) description of New Zealand climate as temperate, Kowhai Bush is subjected to seasonal extremes of weather.

During the winter and early spring (September, October and November) southerly changes can bring sudden showers of rain, hail, sleet and occasionally snow. Snow occasionally accumulated on the bush floor but did not persist for more than two days. Southerly and easterly conditions with associated cold temperatures, wind and rain, often persisted for seven to ten days. Most of the first stages of the breeding period coincided with early spring when the average ambient temperatures were higher than the mid winter low in July (see Appendix 4).

The summer months over which breeding occurred (December and January) were generally mild (see temperature averages in Appendix 4) but characterised by low rainfall and drought conditions. Drought conditions were worsened by frequent strong North Westerly winds which had a marked dessicating effect with temperatures inside the bush often reaching over 30°C. During these drought conditions many undergrowth species died and birds were occasionally seen panting and noticeably lethargic.

2.General Methods

(i) Nestboxes and Tracks.

About 320 nestboxes were distributed along approximately 12km of track throughout both study areas. Nest boxes were designed with the same dimensions and materials as described by Gray (1969). Modifications included fitting a perch just below the entrance hole and making an eliptical hole with a maximum diameter of 20-22mm and maximum width of 36mm. The hole diameter was quite critical because anything larger than this allowed access to stoats (Mustela erminea), which were the chief predator. Holes of this size did not prevent stoat attacks but stopped them taking nest contents. The other modification was a lid tie-down which was made out of rubber and fastened from the bottom of the box to the middle of the lid. The other method of minimising the problem of predation was a trapping programme which lasted for three years.

The tracks were marked with red plastic ties and numbered in a grid pattern so that one could get to any position in the study area quickly. Nestboxes were erected at about 50m intervals along the tracks off to one side so that the observer did not disturb nests when walking up and down the track.

What constituted a preferred nest box site was never determined. However, it appeared that boxes in dry sites with enough low foliage around to enable discreet entries and exits by the birds were used most frequently. In the first two seasons used nest boxes were taken down, cleaned and relocated near the old site. It became apparent that relocating used boxes was not necessary but removing old nests was, as birds would not re-use old nests.

Other bird species did not use nest boxes because of their larger sizes. However, wetas (Hemideina spp Or.Orthoptera) proved to be

significant competitors especially after nestbuilding had finished. Wetas used all boxes but seemed to be especially attracted to nesting boxes. Up to 12 wetas could be found in a box usually just under the lid. Wetas are large (up to 50mm long) and nocturnal. Their size and daytime activity disturbed Riflemen and may have caused desertion after wetas entered the nest bowl. There was nothing that could be done to stop this except evict wetas whenever nest box inspections were made.

(ii) Natural nest sites; Only one of the 14 natural nest sites found fledged young. Sites were found in the dead foliage of Cabbage Trees (Cordyline australis F.Lilliaceae) which hangs under the crown of the tree, in the hollows of rotting timber and in cavities underground including rabbit (Oryctolagus cuniculus) burrows. Natural nests were best found by following nestbuilding or feeding adults or using the intensity of parent's alarm calls as a measure of how close one was getting to the nest site. Because of the poor success of natural nest sites they were not used for data collection except for some nestbuilding data.

(iii) Inspecting nest sites; Sampling parental care systematically throughout the nesting cycle required precise knowledge of the timing of the nesting cycle. The expected lengths of laying incubation and nestling periods were known from Gray's study and these were used initially to gauge when to make nest inspections to record exactly the onset of the incubation, nestling and post fledging periods. During the laying and incubation periods there was some risk of desertion due to observer interference. By approaching the nest quietly and checking to see if there was a parent on the nest before looking inside the nest bowl, the observer could usually avoid being "caught out" near the nest by a parent.

Once it was ascertained that no parents were on the nest a 5mm

diameter veterinary anuscope was inserted into the nest bowl through a hole opened in the top using a pair of tweezers to spread the nest material slightly. Once this was done the first time subsequent inspections were easier but care was needed inserting the anoscope because of the risk of breaking eggs. When the inspection was complete the hole (about 7mm) was blocked off with straw. The birds also usually blocked the hole from the inside with feathers.

(iv) Watching nests.

Almost all data on parental care at the nest were gathered from a hide. Like other native passerines at Kowhai Bush (except the Robin) Riflemen are, with a few individual exceptions, nervous of humans near the nest especially if they have been banded. However, during courtship-feeding and nest building Riflemen were quite tolerant of human presence.

Portable hides were made of heavy hessian which were slung over a wooden frame or erected within 10-15m from a nest with guy ropes tied to surrounding trees. It was not practicable to erect them stage by stage. Instead, hides were set up as early as possible before observation was started with the intention of allowing the birds to get used to them. Access into the hides was achieved from the cover of undergrowth if available or when the bird was in the nest. If the observer was seen entering a hide then a period of 10-20 minutes was allowed to elapse before observations were started.

(v) Nest temperatures.

Nest-air temperatures were measured every three seconds in some nests using a thermistor located amongst the eggs. The thermistor was linked up to a Grant's thermograph which recorded temperature on calibrated pressure

sensitive carbon paper. By calibrating the rate paper moved through the machine with time it was possible to tell when eggs were laid and when birds left the nest by the corresponding drop in temperature.

(vi) Eggs.

Rifleman eggs are extremely fragile and difficult to get out of the nest. Hence about half of the data on egg dimensions were taken from unhatched eggs and deserted clutches. "Fresh" egg weights were taken from first clutch nests as soon as possible after laying and before incubation started.

(vii) Nestlings.

Young under four days old were too delicate to handle. After this age nestlings could be extracted and identified by marking legs and/or wings with a felt tip pen. The rest of the procedure for measuring young is described in section four.

(viii) Banding adults.

Mistnetting Riflemen was difficult compared with other native passerines at Kowhai Bush, because they were rarely attracted to the net using taped recordings of their calls. Recordings of fledged juveniles begging played through alternate speakers worked best. Nets were most successful near nest sites set up with speakers on either side.

The other means of catching adults involved placing a small hand net over the entrance of the nest bowl when the adults were brooding. It was not advisable to use this method during incubation because of the risk of desertion. The method was only used as a last resort and was not used on nests at which data on parental care were gathered.

Anatomical dimensions of adults were recorded as described in section four. Unique colour band combinations with individually numbered aluminium bands were used as part of the New Zealand National Banding Scheme under permit from the NZ Wildlife Service, Department of Internal Affairs. The colour bands were the AA size celluloid "butt-ended" type which were a little too large but were the smallest available in New Zealand. Aluminium bands were also butt-ended AA's and were best crimped together between the fore finger and thumb in a slightly oval shape.

(ix) Day-periods.

Observations of parental care were made as evenly as possible between six equal periods during the day. The length of these periods was calculated by dividing by 6 the number of hours between sunrise and sunset times which were supplied by the NZ Meteorological Office. Average daylengths and average day-period lengths for the month's observations on parental care are shown in Table 1 below (after Powlesland 1980).

Table 1 Monthly average daylength and dayperiod length (hours)

	daylength	day-period length
August	10.4	1.7
September	11.8	2.0
October	13.3	2.2
November	14.6	2.4
December	15.3	2.6
January	14.9	2.5

(x) Assessing weather conditions.

Every time parental care was measured a subjective description of cloud cover, temperature and wind was recorded.

a.Wind. A modified Beaufort scale was used to gauge wind conditions. The Beaufort scale is set out below with the corresponding grouping into the four categories used in this study.

Table 2 Beaufort wind force scale conversion

Wind speed (knots)	Official description	Beaufort	Conversion
0	smoke rises vertically (calm)	0	1
1-3	smoke drifts (light air)	1	2
4-6	leaves rustle,wind just felt (light breeze)	2	2
7-10	wind extends light flag (gentle breeze)	3	2
11-16	raises dust and small paper (moderate breeze)	4	3
17-21	small trees sway (fresh breeze)	5	3
22-27	large branches move (strong breeze)	6	4
28+	trees move hard to walk (near gales and stronger)	7+	4

b.Cloud cover. Four categories were recognised as shown below:

Table 3 Cloud categories and associated conditions

Scale	Description
0	sunny conditions, no clouds in the sky
1	strong sun, cirrus cloud, 80%+ blue sky
2	overcast, 100% cover high to low ceiling cloud
3	rainy conditions: intermittant to continuous

c.Temperature. Three categories were recorded; 0-8°C = cold, 9-20°C moderate and 21+°C = hot.

(xi) Computer analysis.

Data on parental care were recorded onto a portable tape recorder because of the need to keep watching the nest constantly. These data were transcribed onto data sheets, checked and coded onto computer data sheets. Programmes were written to work out hourly rates for the variables used to measure parental effort. Printouts of these data were entered into a micro computer to gain summary data and conduct statistical tests.

(xii) Definitions and rules followed in the thesis.

Parental investment : any investment which reduces the bird's ability to invest in future reproductions (Trivers, 1972).

Parental effort (= reproductive effort) : taken after Hirshfield and Tinkle (1975) as "that proportion of the total energy budget of an organism that is devoted to reproductive processes".

Parental care : the behavioural repertoire of a parent during the reproductive cycle and in this study does not imply anything about energy cost.

Time is given in New Zealand Standard Time and units of measurements are Standard International (SI).

Riflemen refers to (Acanthisitta chloris chloris), Grey Warblers Gerygone igata , Robins to Petroica australis , Brown Creepers Finschia novaeseelandiae and Fantails Rhipidura fuliginosa , all of which are found at Kowhai Bush.

Bush refers to Kanuka (Leptospermum ericoides) forest.

In tables "X" is used as a symbol for the average statistic and "SD" stands for the standard deviation of an average.

SECTION ONE : COURTSHIP-FEEDING

A. INTRODUCTION

Preamble

The female Rifleman lays a huge egg, some 19% of her body weight, which is towards the upper limit of egg size relative to body weight known for birds. The demands of producing such a large egg are compounded in that, during the course of laying her first clutch, an average female lays eggs amounting to about 85% of her body weight in about eight days. From a study of bird weights before and after laying, Perrins (1969) maintained that Passerines lay eggs using daily energy intake rather than drawing from reserves. It seems unlikely that female Riflemen could increase their weight by 85% or the equivalent dry weight of eggs (about 25% of the wet weight, Kendeigh et. al. 1956) before laying. It is also doubtful that the extra nutrients could be stored as equivalent dry weight.

At Kowhai Bush, Riflemen start laying during early spring, probably while the food supply is still limited. Kowhai Bush can be very cold and wet at that time. The average minimum and maximum ambient air temperatures during the Septembers of the two seasons when courtship-feeding data were taken were 3.9°C (SD = 2.4) and 14.7°C (SD = 2.8). The daily average ambient air temperature was 9.3°C and the average precipitation was 101.5 mm. Sleet and hail storms were common and occasionally accompanied by strong polar originated southerly winds. The above factors raise two questions : (1) how does one of New Zealand's smallest Passerines cope with laying approximately her own body weight in nine days during the conditions of early spring? (2) What circumstances enable the female Rifleman to produce a second clutch amounting to about 65% of her body weight over seven days, later in the season? These questions are tackled

in this study of courtship-feeding.

Four hypotheses were investigated in relation to the function of courtship-feeding: (i) the purpose of courtship-feeding is not to provide nutrition but is simply a component of courtship behaviour, (ii) courtship-feeding provides essential elements for egg production (iii) the benefits of courtship-feeding are mainly in providing the extra energy for oogenesis (iv) some combination of hypotheses one to three is involved in courtship-feeding.

Other research

Few studies have tackled the questions involved in the courtship-feeding phenomenon because of the technical difficulties of observing birds continuously in the field, and in measuring the amount of food consumed.

Observation of courtship-feeding in the Laridae is not difficult as the birds are localised in colonies and the feeding rate is relatively low. Hence the actions of many pairs may be sampled at once. Tasker and Mills (1981) estimated the volume of food that male Red Billed Gulls (Larus novaehollandiae) fed to females by establishing the maximum amount of food males could carry. One quarter of the maximum quantity was used as the unit to measure the volume of courtship-fed meals. The sizes of regurgitated lumps of food fed to females were visually assessed. It was concluded that courtship-feeding provided a large proportion of the female's intake.

Royama (1966a) studied courtship-feeding at the nest of Great Tits (Parus major) using observations made from a hide. Courtship-feeding occurred throughout the egglaying and incubation periods. Recording supplementary feeding away from the nest area in Great Tits is very difficult unless the female draws attention to herself by begging. Data

gathered at the nest were used as courtship-feeding away from the nest was infrequent. Royama showed that the male's contributions during laying and incubation were needed for the female to meet the nutritional requirements of egg production. Furthermore, supplementary food taken from the male was essential for the female to meet her maintenance needs while she was spending most daylight hours incubating.

In this enquiry into the courtship-feeding behaviour of Riflemen the amount of food fed to females has been estimated in milligrams of dry weight. The amount of self-fed food obtained by each sex was also noted and enabled an estimate to be made of the male's contribution to the female's total food intake. Another aim was to determine if the rate of courtship feeding peaked at the time of, and correlated with predicted energy demands for, oogenesis. Male Riflemen do not feed their mates before or during laying of second clutches, allowing comparisons to be made between the sizes of first and second clutches, in egg sizes, and laying intervals.

B. METHODS

1. Data Collection

Information on foods eaten was recorded on a Sony portable tape recorder so that birds could be observed continuously. A digital stopwatch was used which permitted the time the bird was out of sight to be recorded as well as the total time elapsed. Hence the time of continuous contact with the bird could be noted. This figure was then used to convert data on self and courtship-feeding into hourly rates.

Almost all courtship-feeding data were taken from the pilot study area

where the mean canopy height was about 2.5 m and the trees were well spaced. Foraging Riflemen could be viewed continuously from 5 to 10m through 8 x 35 Zeiss Jena binoculars. The size of food item sizes was estimated as they were consumed.

Food items were scored on a size scale of 1 to 8. An item of size 1 was about one quarter the length of the bill or less. An item size 2 was between one quarter and one half the length of the bill and so on until a food item twice the length was scored as size 8. Food items could be sized because Riflemen fed themselves (and their mate during courtship-feeding) one food item at a time. Where possible the type of food item was also recorded. All but the smallest food items were held in the bill and broken up before being eaten, greatly aiding size estimation.

Birds were not sampled systematically as individuals or pairs relative to the stage of oogenesis (except after egglaying had begun) because it was not always possible to find a given pair on a given day. Also, there was no way to predict exactly when a particular bird was going to start laying.

Whenever possible courtship and self-feeding behaviour were noted for about 25 minutes. Most birds were colour banded which, together with the Riflemen's obvious plumage sexual dimorphism, greatly helped in keeping track of an individual.

Information noted included:

(i) the number, type and size of self-fed and courtship-fed items;

(ii) the total time a pair spent foraging together;

(iii) the time spent on foraging, preening, nest-building, territorial behaviour, resting and copulation;

(iv) the area covered whilst foraging;

(v) the number of times females begged from or robbed males;

(vi) the proportion of time the bird fed in the top or bottom half of the tree, including the ground;

(vii) a description of behaviours in courtship-feeding, intraspecific territorial behaviour and interspecific interactions.

2 . Sampling Invertebrates to Estimate Calorific and Nutritional Worth

During the courtship-feeding period invertebrates of the size range used by Riflemen were gathered from the pilot study area and from all parts of the substrate in which the birds were seen foraging. Collecting was done using beating boards, by searching bark and ground litter, and by light trapping at night.

The taxa found were Orthoptera : (Weta Families: Heinicidae, Genus Hemideina and Family Rhophadophoridae); Diptera (mainly craneflies, F. Tipulidae); spiders (Or. Opilione, Araneia); Lepidoptera (adults and larvae) and Coleoptera (adults and larvae). These were the groups taken most frequently by the birds.

After sorting by size, the samples were dried in an oven at 60-70°C for 24 hours and then weighed using a Mettler Balance. The average dry weight for size categories 1 to 8 for all taxa combined was worked out using the method for calculating the average for a composite group from those of its subgroups, as described in Walker and Lev (1969). This is a numerical method by which the statistics of a combined group (a size category including all taxa in this case) may be calculated from those of its subgroups.

3. Egg Staining and Egg Measurements

The time taken to form an ovum was calculated using the method described by Grau (1976). Eggs for yolk staining were taken from recently deserted nests and were kept frozen at -20°C before treatment. Grau's staining method was slightly modified to determine the time to form the yolk only. Frozen eggs were dunked in water just long enough for the shell to be removed. The yolks were then placed in 4% formalin and into an oven for 16-20 hours at 60-70°C. After this the yolks were transferred to 6% potassium dichromate for another 16-20 hours at 60-70°C. Grau suggested sectioning stained yolk halves at this stage for examination. However, Riflemen yolks are only about 6 mm across and could not be easily handled or sectioned after being sliced in half. Consequently yolks were mounted in gelatine and then sliced in half. Usually the light and dark rings were easily seen without sectioning. Clarity was improved by washing the yolks in water.

4. Analysis

A. The Calculation of Frequency of occurrence of Food Items of Different Sizes in the Riflemen's Diet

Riflemen were watched on 230 occasions in order to gather information on courtship-feeding. Of these occasions only 50 afforded the opportunity to identify the size of all the food items self-fed. However, the size of food items could be assessed every time courtship-feeding occurred. When not assessed, self-fed food items were scored into two categories : those size 3 or less and those size 4 or larger.

From the records in which the size of all food items were estimated the relative proportions of each size category were calculated from their average frequency of occurrence per hour. Computing the hourly frequencies

of items of different sizes for the remainder of the occasions was done by multiplying the scores of food items size 3 or less and size 4 or larger by the appropriate one of these proportions.

B. Calorific Equivalents of Invertebrates

Values from the literature were averaged in order to convert the observed hourly consumption of food (both self and courtship-fed) to a calorific equivalent.

The calorific value per gram of dry organic matter falls between 19.81 - 26.84 KJ with 23.41 being the most probable value that can be encountered among animals (Ostapenija et. al. 1968). Slobodkin and Richman (1961) and Slobodkin (1962, page 299) noted that "the range of calorific values of tissues of various animals is fairly narrow". Bailey and Riegart (1972) reported an average value for insect tissue of 21.9 KJ g-1 d.w. which falls close to the lower limit of the range quoted by Bursall and Taylor (1980) of 20-29 KJ g-1 d.w. for insects.

A mean figure of 23.54 kilojoules per gram dry weight of invertebrates in the Rifleman's diet was calculated by averaging the figures published in the literature cited in Appendix 1. The figure was calculated using the data reported in the literature in Appendix 1 as well as those figures reported in Cummins and Wuycheck (1971). The calculated value is similar to those averages quoted above and considering that the range of calorific equivalents for invertebrates is probably narrow it is assumed it is a reasonable estimate of the actual calorific equivalent for invertebrates in the Rifleman's diet.

The energy consumed (KJ/Hr) was calculated by converting the numbers of the food items of each size category taken per hour into milligrams per hour using dry weight equivalents, and then to energy equivalents using the calculated conversion factor.

C. Discussion of Field Methods.

The methods described above make the following main assumptions:

(1) that the observer's presence whilst collecting data did not influence feeding behaviour,

(2) that the insects gathered were truly representative of the insects Riflemen fed on, and

(3) that the observations in the field and the procedure for conversion to calorific and dry weight equivalents adequately estimate the actual food requirements of Riflemen.

It is relatively easy to tell when observer presence is influencing the behaviour of Riflemen as the observer quickly learns to recognise when a bird is reacting nervously or atypically. It was easy to keep far enough away from each bird according to its' particular temperament. These distances varied for different birds, although some would not accept any observer nearby.

Although the question of the degree of observer interference must remain unresolved it is felt that there is no significant bias in these observations on Riflemen due to the observer's presence. Clear observations were made easier by the open distribution of the trees on the ground and the complete lack of undergrowth which meant that the observer could move silently while watching the birds.

During courtship-feeding and at other times during the breeding cycle, it was not possible to identify invertebrates consumed to specific level, but care was taken to collect from areas of the ground, bark and foliage on or near the surface to a depth it was judged the Riflemen had exploited. Because invertebrates were collected at the same time of the year that

courtship-feeding was being observed, it seems reasonable to assume that the invertebrates Riflmen were feeding on were also available to the observer. Further, because in this study no bomb calorimetry was performed and an average figure calculated from the literature was used, it is more significant that representative food size categories were adequately sampled.

Food consumption studies may be undertaken using direct and indirect methods. All indirect methods at some stage include estimating the size of prey visually. Royama (1965) used a method similar to the one used in this study to determine the size of food items brought from the habitat to the nest of Great Tits (Parus major) including collecting representative insects and spiders fed to nestlings. Length and diameter were estimated by eye from close range observation into the nest box. The dry weight equivalents were determined from a regression line of insect volume (length x diameter^2) against dry weight measured from collected examples.

Hence Royama's and other indirect methods, involve the observer gauging size by eye twice: at the point of capture and when selecting size representatives from invertebrates sampled in the field. Although the method used in this study involves errors it is no less accurate than other techniques used in the past. Further, any margins of error should be the same for both males and females. Because the main aim has been to make comparisons between sexes, any differences in food requirements and the significance of courtship-feeding should still be apparent.

C. RESULTS

1. Description of Courtship-Feeding by Riflemen

Courtship-feeding takes place when the cock bird feeds the hen during the breeding cycle. In most species courtship-feeding occurs during the prelaying, laying or incubation periods. A certain amount of ceremony may be involved before the food is relinquished by the male. However, there was rarely any ceremony involved in Riflemen courtship-feeding.

Food items were given one at a time. Having found an item the male usually pulverised it and flew to the female who took it immediately. Both birds then resumed foraging. The male often voiced a soft, protracted, chittering just before he gave the food. Sometimes a female chased her mate persistently for large food items although they seldom succeeded in obtaining any food. Another occasional technique used by the female, which rarely resulted in acquiring food, involved chasing her mate away from a site on which he was spending some time extracting a food item.

During the courtship-feeding period copulation was seen 14 times. Copulation began about 12 days before first oviposition and finished at the start of incubation. Mounting occurred immediately after courtship-feeding on four occasions. During mounting the female adopted a lowered posture and gave a call like that of juveniles begging for food. It was not possible to tell if cloacal contact had been made. The only behaviour that could be construed as ceremonial occurred on two occasions when the same male was seen to present its partner with a feather and on another occasion a piece of moss. The female manipulated these in her bill before discarding them and resuming foraging.

From several days before the first oviposition and throughout laying, the female frequently appeared lethargic in her movements compared with the

male. Her foraging efforts were noticeably less persistant than his and she spent periods of up to twenty minutes just perching. During these periods the male continued to forage at its usual rate returning to the female to feed her. After an area about the female had been systematically searched by the male, the pair generally moved on and the process was repeated.

2. Weather Conditions and Sampling Description

Observations were made during the months of September and October in 1982 and 1983. The average September temperatures for these years at Kowhai Bush were 8.6°C (SD = 6.4) and 9.0°C (SD = 5.8) and during October 9.2°C (SD = 6.0) and 9.4°C (SD = 6.4). Monthly rainfall was 47mm and 156mm respectively. Data were collected regardless of weather conditions, except for two days when rain was very heavy.

Twenty nine different pairs were sampled over both seasons (Table 1). In the 1982/83 summer, 16 of the 17 breeding pairs in the pilot study area population were sampled and one pair from the main study area. During the 1983/84 season, 14 of the 16 breeding pairs in the pilot study area were used for data collection. These figures reflect the proportion of the total population sampled, as all the breeding birds used nest-boxes. Not all pairs were sampled the same number of times.

Table 1 Distribution of courtship-feeding sampling between different individuals and pairs

	Two day intervals before(-) and after(+) 1st oviposition										
	-6	-5	-4	-3	-2	-1	+1	+2	+3	+4	+5
Pairs	7	4	6	13	8	13	20	19	18	11	6
Males	7	2	5	12	7	9	15	14	17	8	2
Females	5	4	2	7	7	7	15	13	15	10	3

Total number of occasions birds were watched = 230
Total number of different pairs watched = 29
note: the first egg laid occured in interval "+1"

The average time spent following birds for collecting data on courtship-feeding was 24.00 min (SD = 9.5, N = 209) and the average time spent sampling self-feeding was 21.7 min (SD = 8.6, N = 212). Both kinds of data were usually collected concurrently. These averages differ somewhat because of the greater ease of continuously keeping track of courtship-feeding as opposed to self-feeding. Data from samples lasting less than 7 minutes were omitted.

3. The Calculation of Calorific Equivalents of Invertebrates in the Riflemens' Diet

The frequency distribution of identified invertebrates eaten during courtship-feeding is shown in Figure 1-1. These represent 5% of all the food items seen taken by Riflemen during courtship-feeding and illustrate the range of taxa taken but not necessarily their relative importance. Consequently, in determining calorific equivalents, the taxa in the diet were assigned equal importance in calculating the average weight of each food size category. Any errors arising from doing this should apply to females and males alike if there was no difference between their diets with respect to preferred taxa. Types of food taken to the nest did not differ between parents (see section three) which supports the view that male and female feeding ecology was similar.

The number of food items seen taken of size four or less made up most of the total items observed taken by Riflemen during courtship-feeding (Figure 1-2). These figures reflect the availability of different sized food items to the birds. Large items are easily seen when found by a Rifleman and are made more noticeable because the bird spends some time breaking them up before consuming them. Thus the sizes of food items most frequently taken by Riflemen are adequately represented in the collected

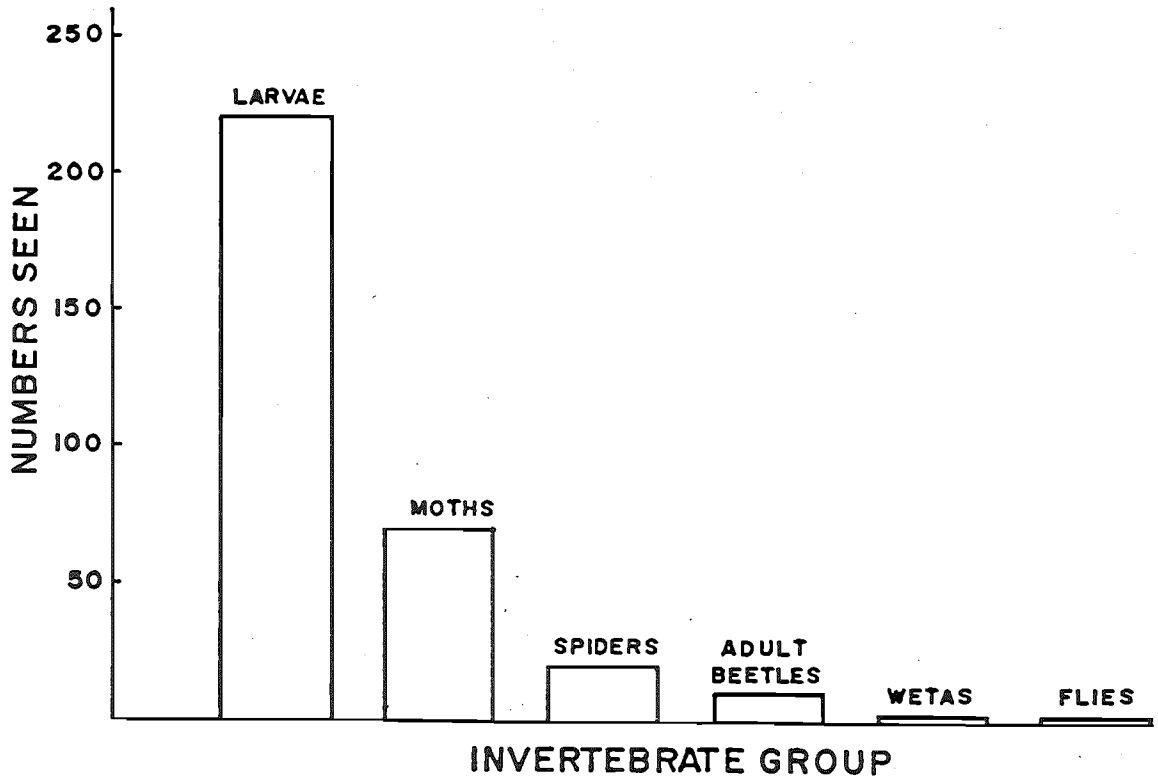


Figure 1-1 The total number of identified invertebrates consumed by Riflemen during the courtship-feeding period.

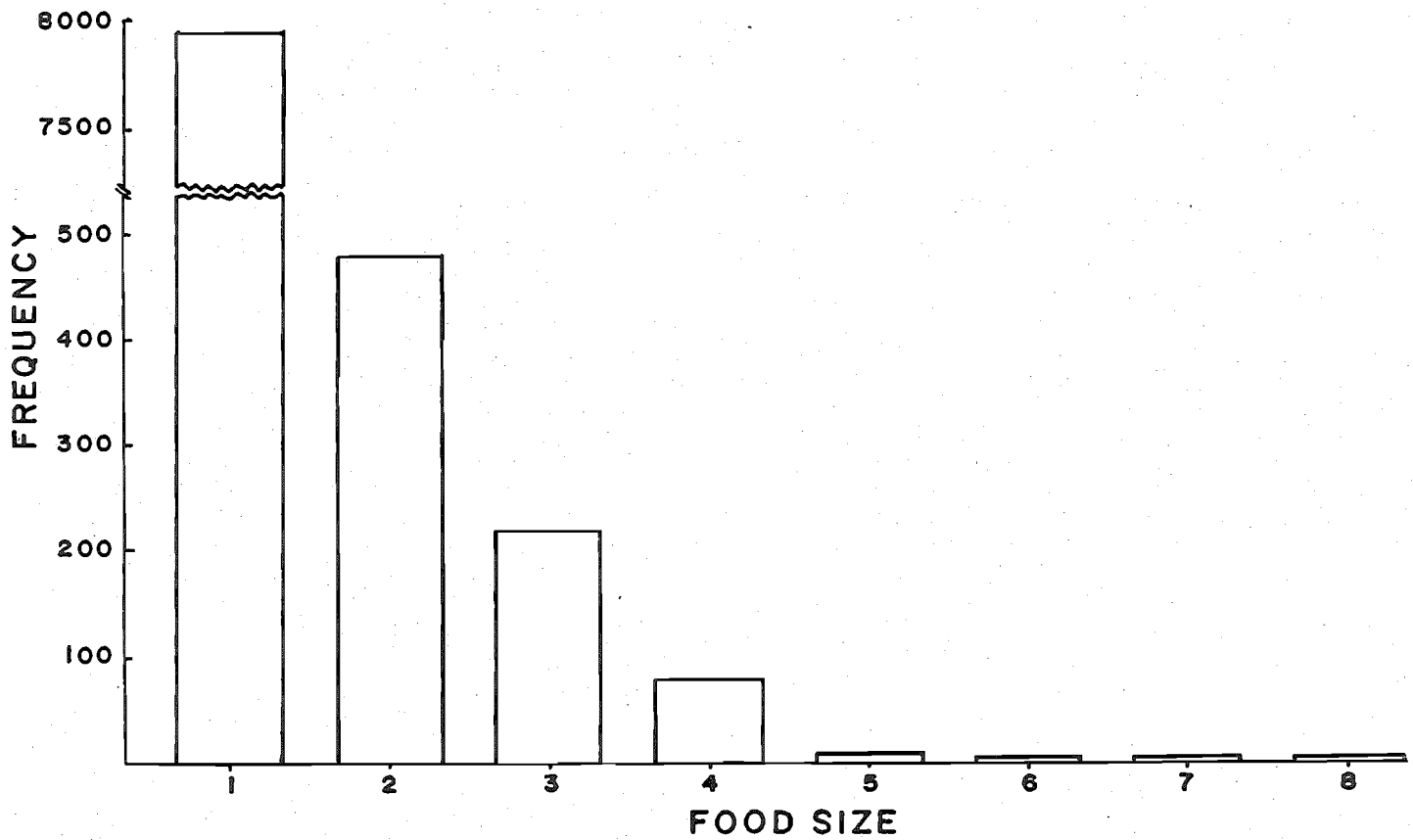


Figure 1-2 The number of food items in each size category seen consumed by Riflemen during the courtship-feeding period.

Note : The size categories equate to food items of the following lengths : 1 = 3mm, 2 = 6mm, 3 = 10mm, 4 = 12mm, 5 = 16mm, 6 = 19mm, 7 = 22m, 8 = 26mm

samples (Table 2). In calculating the average weight of large prey, Dipterans or Coleopterans of size four or greater were not included because Rifleman were never seen eating such large examples of these insects.

Table 2 Average dry weight (mg) of invertebrates consumed by Riflemen

Size	1	2	3	4*	5*	6*	7*	8*
Mean	1.3	4.7	10.3	21.4	46.4	68.4	87.1	119.3
SD	0.5	3.4	6.4	10.9	24.2	29.7	47.6	69.3
N	164	127	132	75	59	40	29	17

note:* indicates figures calculated which excluded Dipterans and Coleopterans > size four as these did not occur in the Riflemen diet.

4. Time Budget Data:

The average proportion of daylight hours that males and females spent in contact with each other during the period ten days before the first oviposition to the end of egg laying, was 91.2% (SD = 21.2, N = 159). This figure is based on 63.6 hours of observation. Males and females spent similar proportions of their time foraging; 98.6% (SD = 4.6) and 97.4% (SD = 9.5) respectively.

5. Comparisons Between First and Second Clutches

A. Egg size

Courtship-feeding does not occur before or during the laying of second clutches. If courtship-feeding is important for the nutritional requirements of oogenesis, it is possible that second clutch eggs would be significantly smaller than first clutch eggs. They were not - the maximum lengths and breadths of eggs were measured to the nearest 0.02 mm (Table 3). Most eggs were from deserted clutches or were infertile eggs left behind after young had fledged.

Table 3: The dimensions of Rifleman eggs (mm)

	x	SD	n
A. First Clutch			
length	15.92	1.44	84
width	12.47	0.40	83
B. Second Clutch			
length	15.51	0.70	37
width	12.47	0.32	37

There was no significant difference in length ($t = 2.11$, $P > 0.05$) and maximum breadth ($t = 0$, $P > 0.05$).

B. Clutch sizes

The presence or absence of courtship feeding might affect the maximum number of eggs laid in a clutch. First clutches were significantly larger than second clutches (mean size of first clutches, SD: $X = 4.4$, $SD = 0.5$, $n = 106$; second clutches: 3.8, $SD = 0.6$, $n = 41$; $t = 5.68$, $P < 0.001$).

C. Laying intervals

Courtship-feeding could affect the interval over which eggs are laid. Regular inspection of nests enabled the day on which new eggs appeared to be recorded. The time of the day when nine first and two second clutch eggs were laid was recorded by noting when nest air temperature rose. This was measured by a thermistor placed in the feather lining at egg level. The thermistor was linked to a Rustrak thermograph which recorded the temperature every three seconds. Riflemen do not usually incubate during egg laying. Eight first clutch eggs were laid between 0630-0730 hours and one at 1030. Two second clutch eggs were laid between 0400 and 0430 hours.

For the purposes of calculating laying intervals, the appearance of a new egg was taken to mean that it had been laid at 0700 on that day. The mean interval between laying consecutive eggs in first clutches was 2.1 days ($SD = 0.6$, $n = 116$) and in second clutches 2.1 days ($SD = 0.7$, $n =$

14). However, it was not unusual to record an interval of longer than five days between egg laying in second clutches but rare to record such an interval in first clutches. Incubation was delayed five times (15%) in second clutches and 13 times (17%) in first clutches. One pair delayed incubation of their second clutch for 5 days after the last egg was laid and still successfully fledged young from all the eggs. The mean length of time of delay when it occurred in first clutches was 2.3 days (SD = 1.0, n = 13) and in second clutches 2.4 days (n = 5).

In the 1982/83 season there were two cases of delayed incubation. It was found that courtship-feeding continued for four days after the last egg was laid in each instance. It is likely that courtship feeding occurred in the other cases of delayed incubation observed in previous seasons.

6. The Amount of Courtship-Feeding

A. The Frequency of Courtship-Feeding.

There was a gradual increase in the mean hourly frequency of courtship-feeding until the rate peaked during the interval between the day the first egg was laid and the day after (Figure 1-3). There was no significant drop off from this peak throughout the rest of egg laying until the start of incubation when courtship-feeding stops altogether. Hence the abrupt ending at the fifth two day interval shown in Figure 1-3. The number of copulation attempts is shown above each interval plot. Ten of 14 copulations occurred after the first egg was laid.

B. The size of food items fed to females

The mean visually-assessed size index of food items in courtship-feeding was 3.75 (SD = 1.33, n = 686) and did not vary

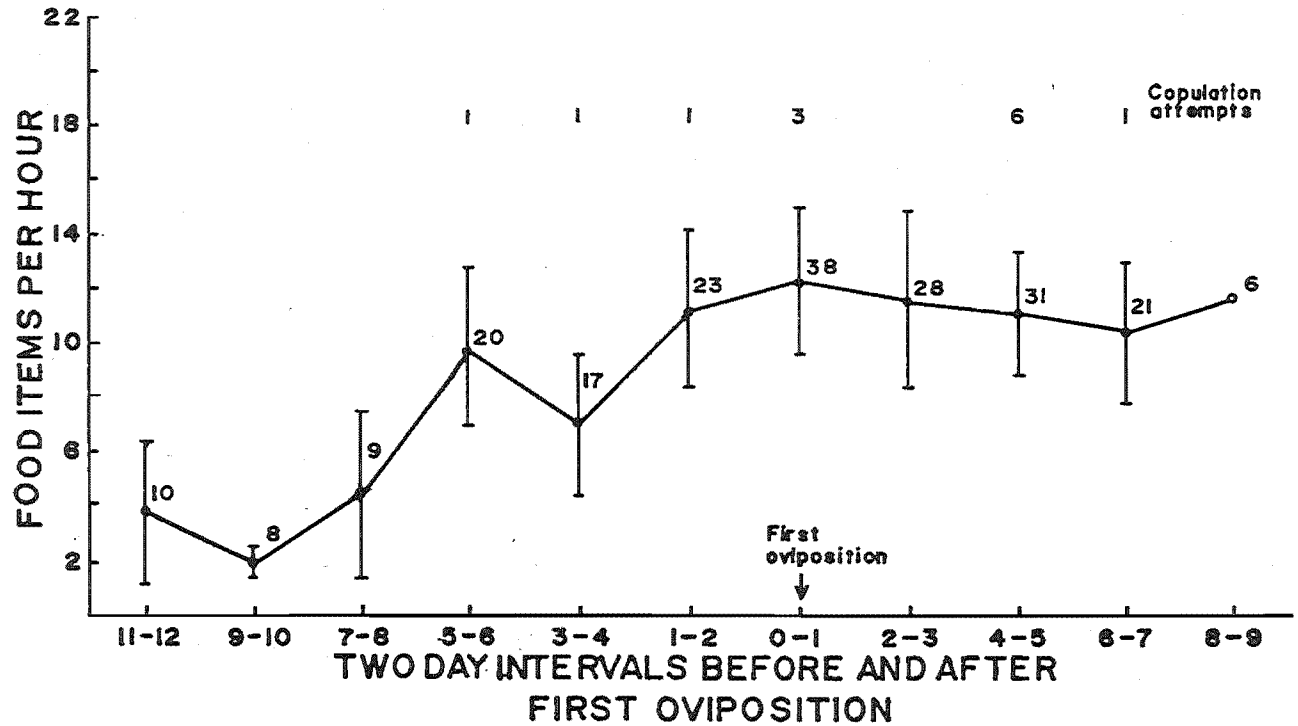


Figure 1-3 Average courtship-feeding rate in Riflemen (95% confidence intervals, sample sizes indicated).

significantly throughout the courtship-feeding period (Figure 1-4).

C. Dry Weight and Calorific Equivalent of Foods.

Significant variation occurred in the amount of food (dry weight) given by the male during courtship-feeding (Figure 1-5, Kruskal-Wallis ANOVA, $H = 51.83$, $P < 0.001$). Consequently, an analysis of consecutive pairs of all samples was conducted using the Mann-Whitney U Test. There was no significant difference between the distributions of any two consecutive two day samples except between intervals (0-1) and (2-3) after first oviposition ($U = 705.5$, $P < 0.05$), implying there was generally no obvious increase-decline pattern in the amount of courtship-fed food over the courtship-feeding period. However, there was a significant difference ($P < 0.05$) between nearly all early intervals and intervals (2-3) and (4-5) following first oviposition. Other significant differences following the start of laying occurred between intervals (2-3) and (6-7) ($U = 420$, $P < 0.05$) and between intervals (4-5) and (6-7) ($U = 436.5$, $P < 0.05$) but not between intervals (2-3) and (8-9) or intervals (4-5) and (8-9). However, the sample size in interval +5 is small. Thus it appears that the peak in courtship feeding occurs about four days after first oviposition.

Figure 1-5 shows the estimated mean hourly rate of courtship-feeding expressed in mg dry weight and kJ. The average hourly rate of dry weight food based on all samples over all the two day intervals was 247 mg dry weight ($SD = 176$, $n = 196$) or 5.80 kJ ($SD = 4.17$, $n = 195$).

7. Amount of Self-Fed Food and Total Consumption.

A. Females and Males.

Females and males were watched on 97 and 106 occasions respectively and of these 70 occurred consecutively. Thus it is reasonable to assume that, in most instances, any effects on food availability of habitat

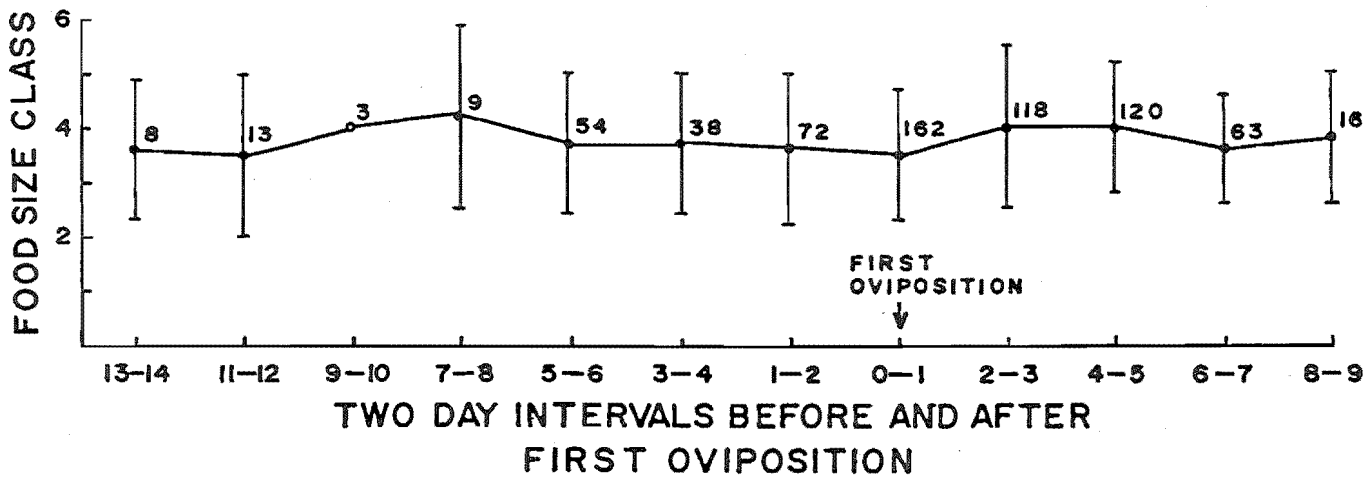


Figure 1-4 The average size of courtship-fed items (± 1 SD, sample sizes indicated).

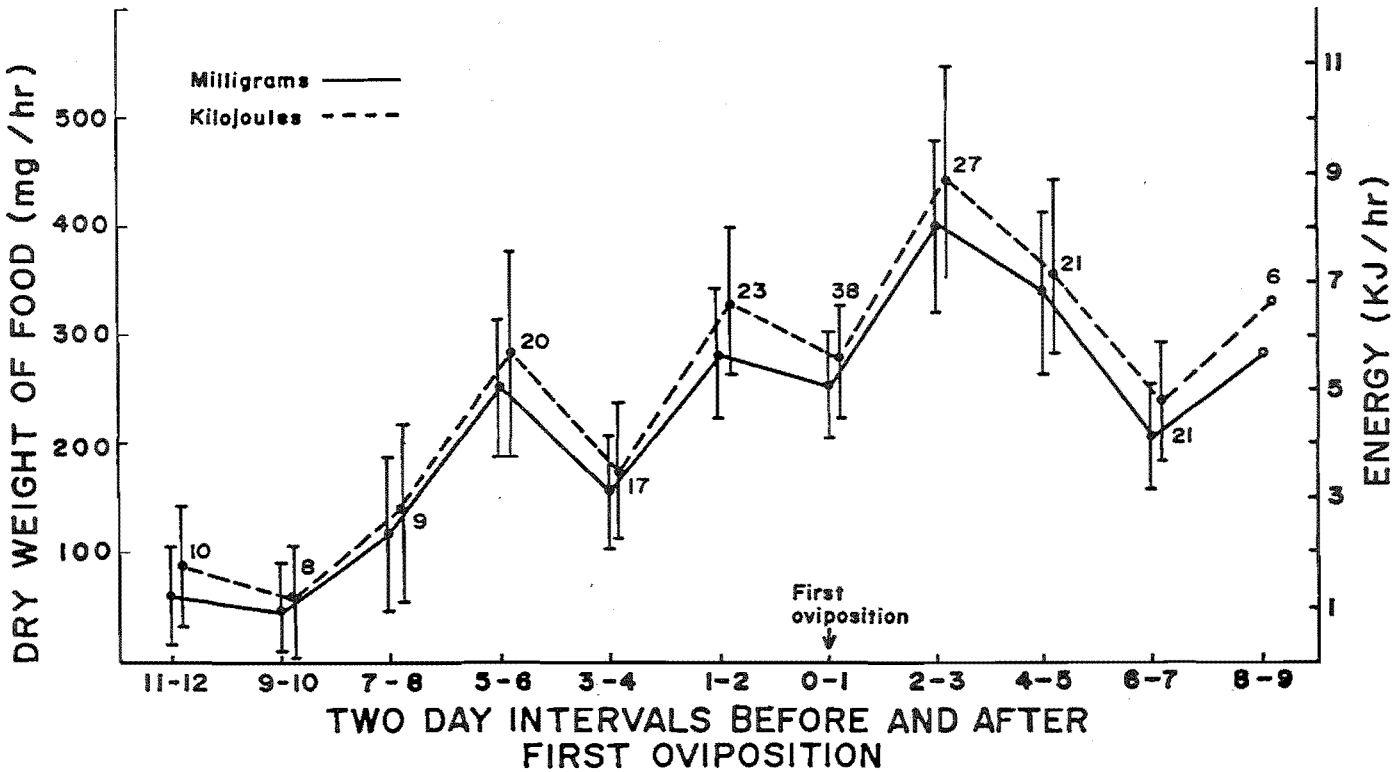


Figure 1-5 The average amount of food delivered to female Riflemen during courtship-feeding (95% confidence intervals, sample sizes indicated).

quality or weather applied equally to males and females. Overall, females fed themselves slightly but not significantly more per hour than did the males (t Test, $P > 0.05$; Figure 1-6). This pattern was fairly consistent throughout the courtship period. However, on average the total food intake of females, including that due to courtship-feeding, was significantly higher than that of the males ($t = 7.455$, $P < 0.001$; Figure 1-7). Although males ate less, they collected significantly more food than females ($t = 4.952$, $P < 0.001$).

B. The Proportion of Food Gathered and Eaten Attributable to Courtship-Feeding.

From the average figures of total female consumption and the corresponding mean figures for courtship-feeding (i.e. data taken concurrently) the proportion of the female's consumption due to courtship-feeding has been calculated in kJ (Figure 1-8). The courtship-feeding fraction, calculated using averages for data taken over the whole period, is 35%. The proportion of all the food gathered by the male and fed to the female was 42%.

C. Nitrogenous Nutrient in Courtship-Feeding.

Nitrogen makes up about 8.6% by weight of insect tissue (J.W. Wightman pers. comm.). Thus the male feeds the female about 21.2 mg/hr of nitrogenous food. The females average hourly rate of self-fed nitrogenous material is about 36 mg/hr, implying that courtship-feeding boosts the female's nitrogenous intake by more than half.

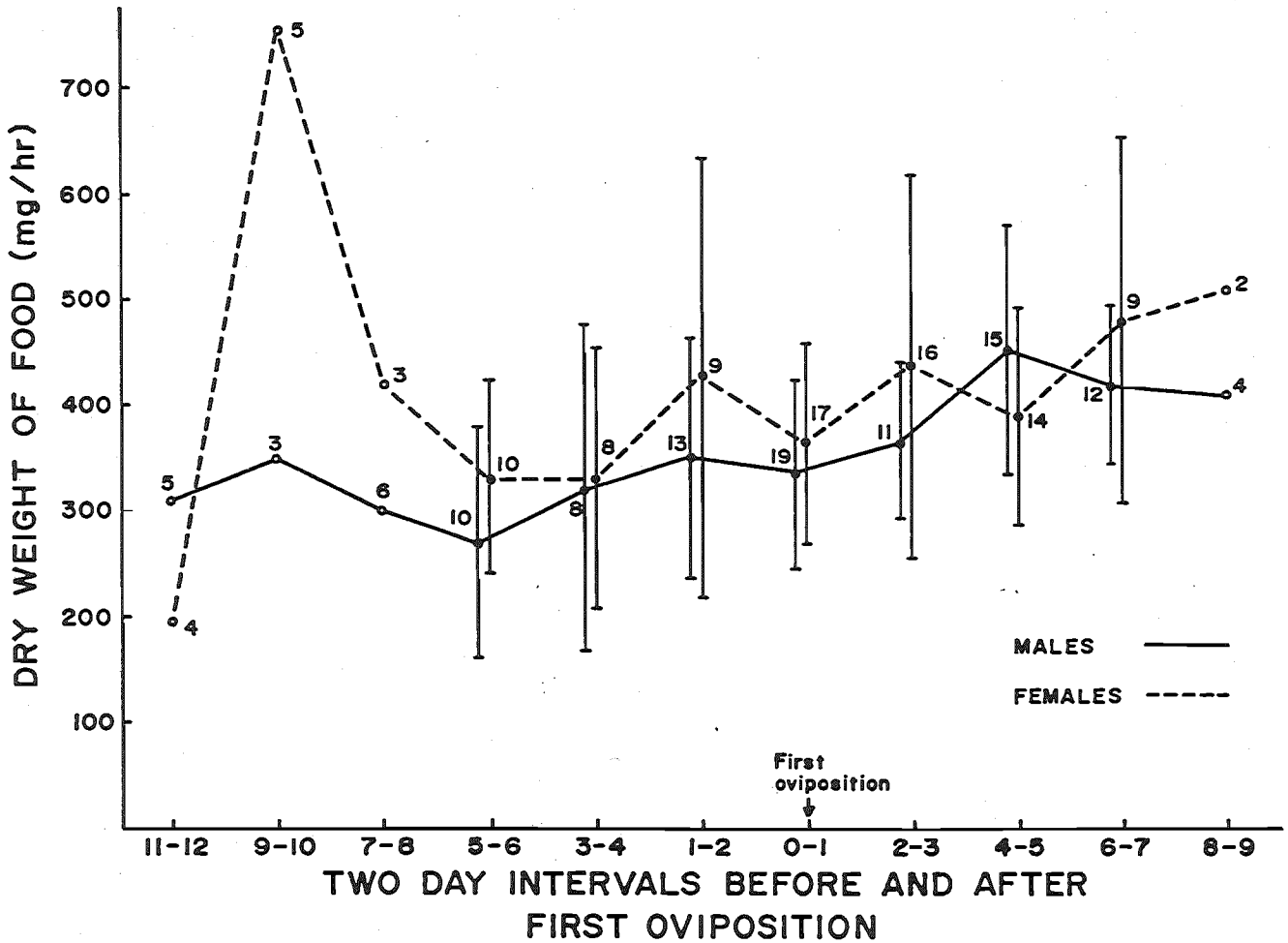


Figure 1-6 The average rate of self-feeding for Riflemen during courtship-feeding (95% confidence intervals, sample sizes indicated).

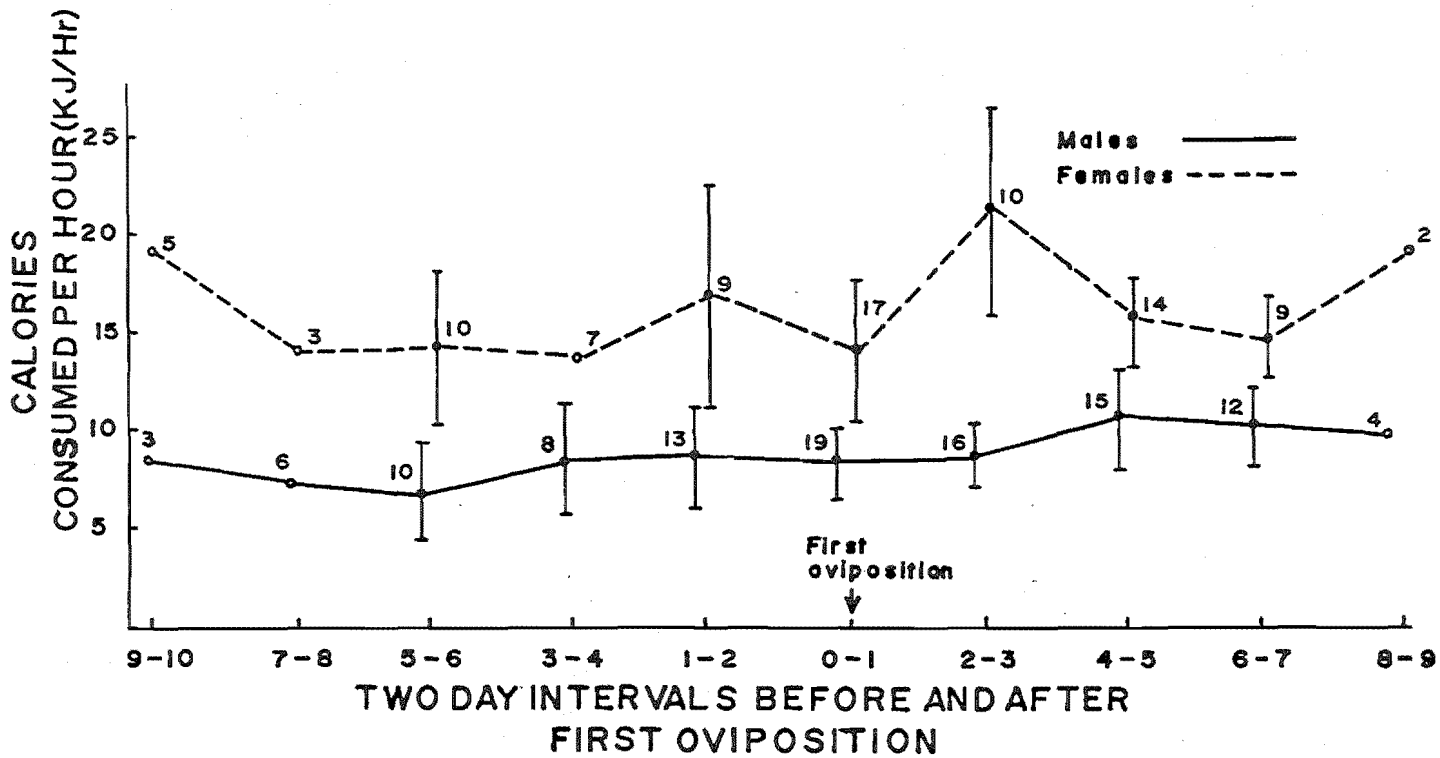


Figure 1-7 The average total energy intake for Riflemen during courtship-feeding (95% confidence intervals, sample sizes)

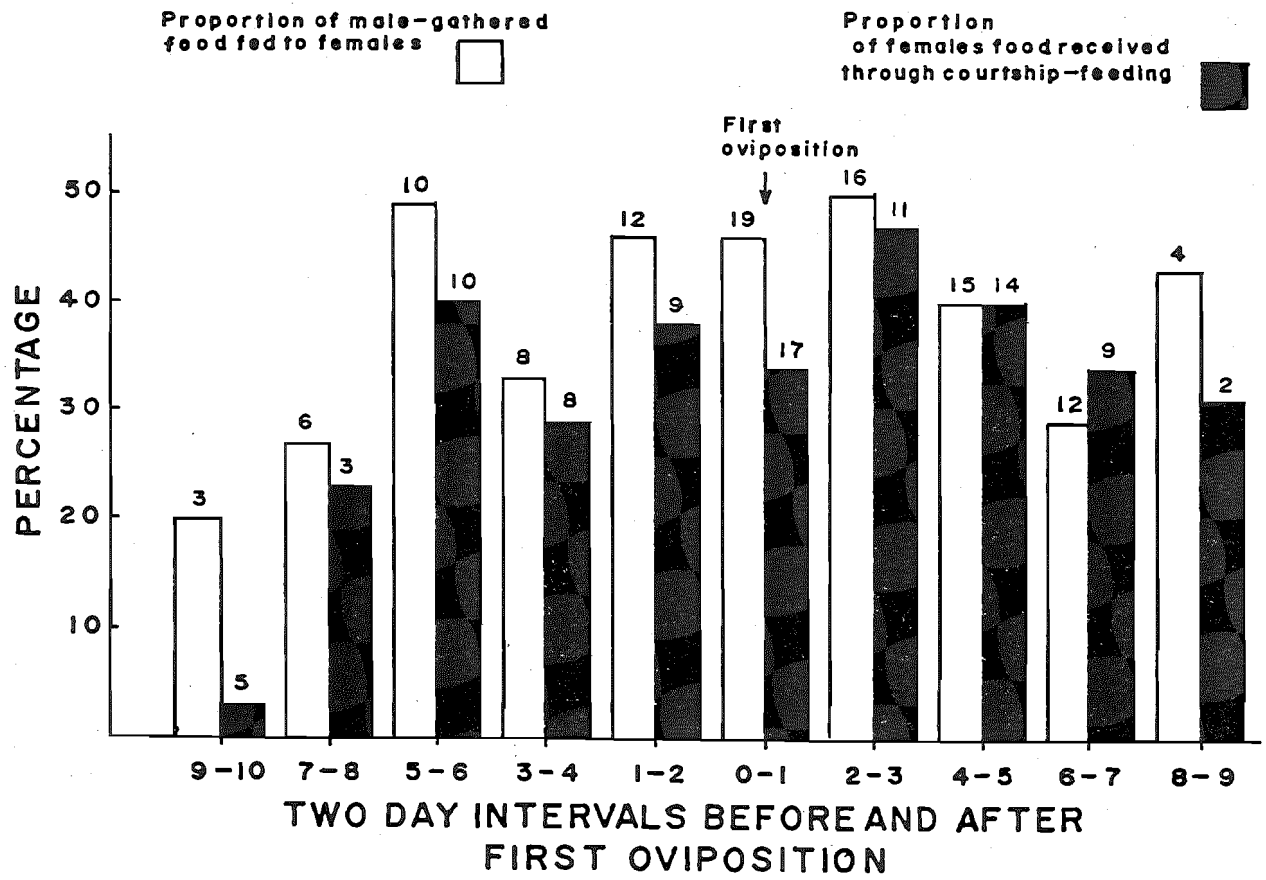


Figure 1-8 The proportion of Riflemen's diet supplied by courtship-feeding (sample sizes indicated).

8. Yolk Staining and the Time Required to Form Eggs.

Four eggs were successfully stained, three from first clutches and one from a second clutch. All four showed three light and four dark concentric rings which were centred about the white (primordial) yolk. The lipochrome (yellow pigment) of yolks is only laid down during the rapid phase of yolk development (Needham 1963). The light and dark rings correspond to night time and day time yolk formation respectively (Grau 1976); thus Riflemen egg yolks take about three and a half days to form which is similar to the three to four days estimated by Kendeigh (1941) for House Wrens (Troglodytes aedon). House Wren eggs weigh 1.53 g when freshly laid which is almost the same weight as unincubated Riflemen eggs ($X = 1.34g$, $SD = 0.10$, $n = 35$).

Powlesland (1980) estimated that Robins (Petroica australis) at Kowhai Bush took one and a half days to form the albumen and shell, which he took to agree with the single day expected of passerines with a 24-hour laying cycle (Gilbert 1971; Ricklefs 1974; Scott and Ankney 1979; Wood-Gush and Horne 1970).

Unlike most passerines which lay every 24 hours (Perrins 1969), Riflemen lay an egg every 48 hours. It is assumed that albumen and shell formation takes about 48 hours in Riflemen. This is likely given the small size of a Rifleman and the fact that it is laying a large egg of about 19% of the female's body weight. Also, the calculated time for Rifleman yolk formation agrees well with those of other small passerines which usually take 3 or 4 days (King 1972). Hence it is likely that the extra time involved in the Rifleman's exceptionally long laying cycle is taken up forming the shell. In domestic hens the albumen and shell take the longest time of any of the stages in egg formation in the oviduct (Brody 1964).

Furthermore, most of the CaCO3 required for shell formation is probably drawn from the diet. This is true of domestic hens where 60-75% of the calcium in the shell comes from ingested calcium and the rest from body stores (Comar and Driggers 1949).

Depending on whether one assumes that albumen and shell formation takes one or two days, egg laying and the associated energy and nutrient demands take about thirteen to thirteen and a half days in Riflemen : from the laying of the last egg of a five-egg clutch to the start of yolk formation of the first egg (Figure 1- 9).

9. Estimating the Cost of Egg Production to Parents

A. Maintenance Energy Requirements.

The average amount of food that males ingested over the courtship period was calculated as 362 mg dry weight/hr (equivalent to 8.557 kJ/hr).

Most courtship-feeding occurred during the month of September. The number of hours of visibility during this month were calculated by finding the mean number of hours between sunrise and sunset and adding thirty minutes for the 'half-light' before sunrise and after sunset. Riflemen foraged in these half-light periods. The average number of available foraging hours per day during this month was 12.28. The weight of dry food required per day for maintenance of male Riflemen was calculated by multiplying the hours available for foraging by the average rate of self-fed food (mg d.w.) which came to 4.445 g per day.

These figures for dry weight of food required for maintenance cannot be converted into energy units and used in energy budget-type calculations because the conversion factors in literature include the energy released in burning chiton, which is probably indigestible. The calculated energy requirements for maintenance is certainly an overestimate as Riflemen were often observed regurgitating hard parts.

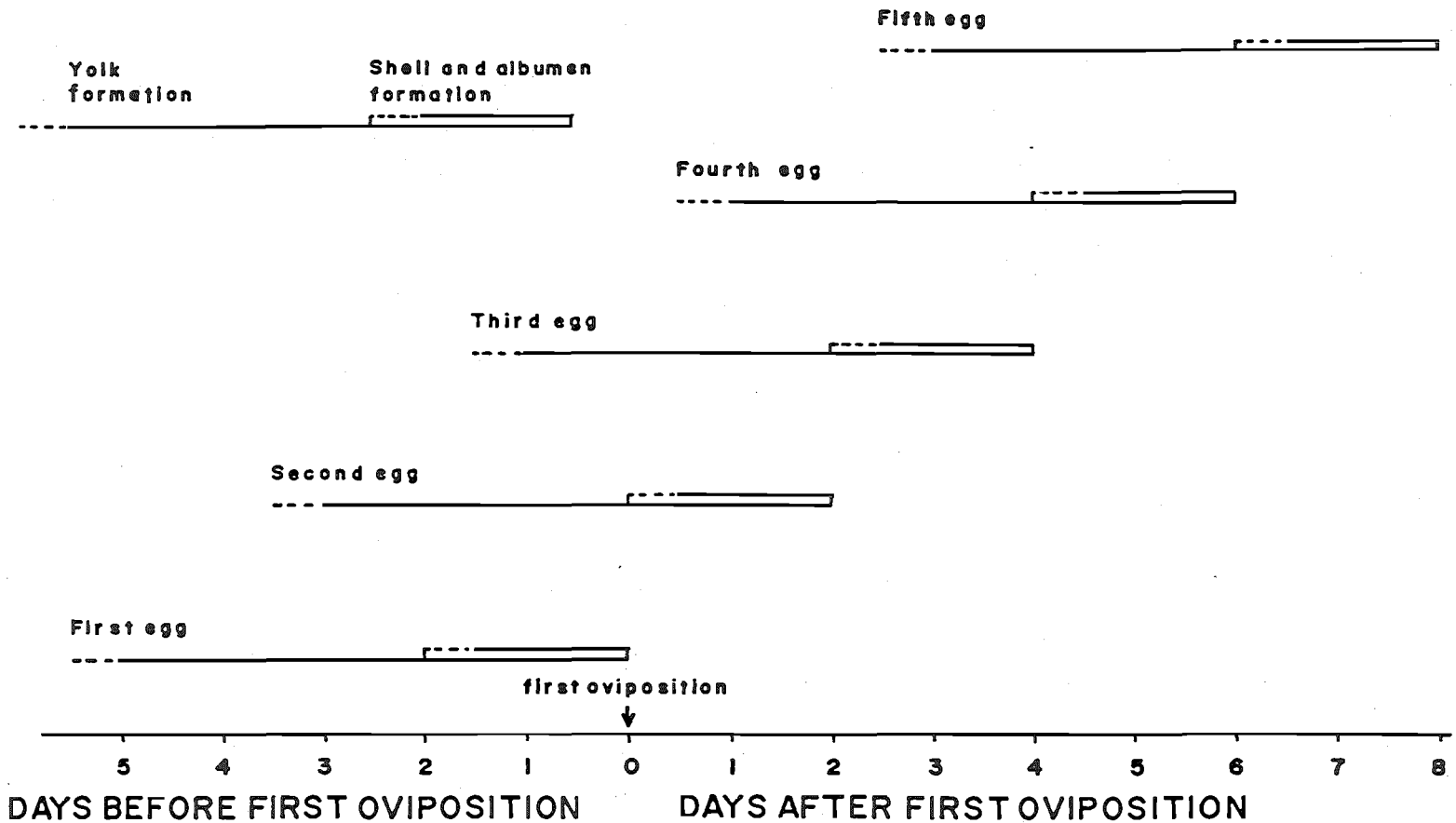


Figure 1-9 Hypothesised developmental sequence of a five egg Rifleman clutch.

Maintenance energy for birds is related to weight by the following relationship $E = k\ W^{0.73}$ where E = maintenance energy, W = weight of bird, k = constant (Brody 1964). This relationship was determined from research done on domestic chickens. However, Petrusewicz and Macfadyen (1970) state that most metabolic parameters vary with weight raised to the power of 0.75.

Taking the mean adult weights of Riflemen, the relationship above may be used to estimate the maintenance energy needs of the non-laying female using the figure for male maintenance needs. The difference in the females' maintenance requirements as compared with that of the males, may be calculated using Brody's formula:

let female adult weight = 6.98g

let male adult weight = 5.64g

Then from Brody's formula -

male maintenance energy = $k\ (5.64)^{0.73} = k\ 3.53$

female " " = $k\ (6.98)^{0.73} = k\ 4.13$

therefore the increased maintenance need of the female

$= [(k4.13 - k3.53) / k3.53] \times 100$

$= 17\%$

given male maintenance food = 4.445 g dry weight/day

then female maintenance food = $4.445 + (0.17 \times 4.445)$

= 5.201 g dry weight/day.

Females self-fed dry weight food = 5.121 g/day which about equates with the predicted amount above. This implies that the extra nutritional and energetic demands for egg laying are met by the 3.033 g dry weight/day fed in courtship-feeding.

D. DISCUSSION

1. Sources of Variation in Results

Two main sources of variation can be identified: that from sampling different birds and that from birds existing in different habitats. Birds probably varied in their ability to gather food because of differing experience between individuals and varying strategies of foraging behaviour which continually changed in time and space. Habitat quality probably varied as a function of time of day, weather, season and other unknown factors.

Results from this study showed that foraging effort returned a variable amount of food. Thus some of the nutritional significance of courtship-feeding may be not only in solely increasing the volume of the food eaten by the female but also in minimising any fluctuations in food intake. The resulting improved consistency of the volume of food available to the female could be very important in raising the energy intake to a level high enough to allow egg production. In other words, the fluctuations in food intake which accompany a patchy environment with only one bird's foraging efforts are minimised with courtship-feeding.

2. The Estimation of Maintenance Requirements and the Significance of Courtship-Feeding

Gibb (1957) calculated the daily dry food requirements of the Coal Tit to be 2.4g. Because the Coal Tit weighs about two and a half grams more than a male Rifleman, one might expect Gibbs' estimate to be greater than the estimate made for the Rifleman. Considering the methodology used by Gibb and in this study, there are probably many possible reasons for the difference. One of these is likely to be that Gibb's birds were captive

and would not have had the same energy demands as free-ranging Riflemen. For example, there would have been considerably less energy required for flight as the tits were kept in a cage 0.915m x 0.915m x 0.610m. Nor were they embarking on a breeding season with its additional energy demands. The Tits' diet in Gibb's feeding trials included seeds and nuts. These had higher calorific values than the one used to convert the invertebrates consumed by Riflemen. Further, Tit's diet would not have had the same indigestible fraction of chitin as the Riflemen's wholly invertebrate diet.

The calculation of the importance of courtship-feeding is conservative. The reason is because the estimate of the amount of the food the male required for maintenance was probably too large. So too was the subsequent estimate of the female's maintenance needs because the observed consumption by males must have been additional to that needed if they were not spending time and energy in courtship-feeding.

Courtship-feeding is important to the female as it accounts for about one third of her total food intake during the pre-laying and egg-laying periods. Similarly, the male Great Tit in Japan contributes about 33% of the female's food during the same periods (Royama 1966b).

The males' contribution of about 40% of the food they collected to females was probably related to their gathering significantly more food per hour than the females. However, males are not necessarily more efficient foragers than females at other times. Rather, males probably work harder at foraging than females during the courtship-feeding period.

Food from supplementary feeding boosts the female's total food intake above maintenance level requirements (which her own efforts achieve) to meet the extra nutritional demands of egg production. For a foraging female Rifleman there must be a point where extra foraging effort will detract from the benefits of courtship-fed food. The cost benefit trade-off between extra foraging and relying on courtship-feeding would be

a particularly important consideration if the relationship between increasing foraging effort and food ingested was one involving diminishing returns. Thus the female's strategy was to gather food for maintenance requirements rather than expend extra energy in foraging to supply the additional demands for egg production because the male could meet this demand adequately.

Observations on gravid females support the above reasoning. During the egglaying period the females were much less active than at other times. They tended to remain perched while the males foraged actively about their positions and periodically returned to feed them.

3. The Efficiency of Courtship-Feeding

Males selectively fed females on average size four food items whereas 90% of items gathered in foraging were size one (see Figure 1-2). The saving in energy by males feeding fewer large items rather than many small ones was probably important for the males. One item of size four was calorifically equivalent to about 16 items of size one. As the males usually flew to females to feed them, the fewer trips a male made to feed large items must have represented a considerable energy saving in comparison with small items brought individually. Efficiency considerations may have been the reason that there were no significant changes in the average size of courtship-fed items over the courtship period (see Figure 1-4).

Riflemen pairs also conserved energy during the courtship-feeding period by spending over 90% of the daylight hours in continuous contact, which was helped by an almost constant exchange of single note calls. Staying in contact with the female would have greatly aided the male in finding the female in order to feed her.

Courtship-feeding may interrupt the female's own foraging efforts and reduce her foraging efficiency Krebs (1970). He showed that the total food intake of the female Blue Tit during courtship-feeding is about two and a half times her mean intake during normal foraging. It was not possible to compare the female Riflemen's foraging returns with and without courtship-feeding. However, it is highly unlikely that the female suffered a loss in foraging efficiency with the male feeding her. Krebs' results support this idea. Except for female Blue Tits begging, the process of courtship-feeding is very similar between the two species, with the male flying food to the female and the female only briefly stopping foraging to take it.

4. Nutrient requirements and Egg Production

The significance of courtship-feeding may lie in more than just supplying the female with extra calories to produce eggs. More than 90% of avian egg shell is composed of calcium carbonate (Needham 1963). Therefore, the increased demand for calcium might be of equal or perhaps greater importance in egg production.

If most of the calcium for shell formation is drawn from the diet (Comar and Driggers 1949) then mineral supply might present the greatest limitations to the female's ability to produce eggs. Courtship-feeding would be essential if the female could not meet demands for calcium from her own foraging efforts.

The same argument holds for the extra demands for protein to produce eggs, as about 16% wet weight of eggs is made up of protein (Needham 1963). Given that Rifleman eggs are relatively large, the approximately 50% of extra protein supplied in courtship-feeding is probably essential, especially as it is unlikely that such a small bird could store this as

extra weight and still fly efficiently.

5. The Timing of Laying and Courtship-Feeding

A. Laying Cycle

The Rifleman's unusual two day laying interval minimised the demands on the female at any given time. From Figure 1-9 it can be seen that with a two day laying interval there were only two yolks being formed simultaneously, one being at a very early stage of development. There would be two consequences of female Riflemen laying every 24 hours: (i) the albumen and shell must be produced in 24 hours as the shell gland can only accommodate one ovum at a time; and (ii) three yolks would need to be forming concurrently because yolk formation takes three and a half days. Furthermore, two of these would be at a relatively advanced stage of development.

King (1972) described a sine wave model for the energy demands during the production of eggs which predicts that the peak calorific demand for producing eggs is related to laying interval (P) and calories per egg (A) as follows:

$$kJ(peak) = 2A/P$$

For Riflemen, a 48-hour laying cycle as opposed to a 24-hour cycle (typical of passerines) halves the peak energy demand on a female and on a courtship-feeding male. Thus it is likely that the Rifleman's 48-hour laying cycle alleviates the energy and nutritional demands on a pair at the peak of an egg's production.

6. The Relationships between Double Broodedness, Timing of Breeding and Monogamy

How can Riflemen produce second clutches without the benefits of courtship-feeding? The energy requirement for second clutches is less than that for first clutches because the average second clutch was 0.6 of an egg smaller than the average first clutch. Second-clutches are usually laid during the last half of November and the first week of December, i.e. in the middle of spring when food availability is probably at its peak. Thus, despite the demands of fledged but dependant first-clutch offspring and maintenance needs, it is hypothesised that energy requirements for egg production were probably more easily met with a greater abundance of food at this time of year.

An important benefit of courtship-feeding included increasing seasonal productivity of offspring. Courtship-feeding probably allowed the female to meet the nutrient demands of egg production early enough in the season for her to have time later on to rear a second brood. So the male's early investment of time and energy in the first clutch through courtship-feeding significantly boosts his own productive potential, as well as the female's ability to form eggs for the first clutch.

The advantage of courtship-feeding in allowing the production of second broods implies that there is an obvious advantage to the male to form a permanent and stable monogamous pair bond as early as possible. Rifleman pair-bonds are formed as soon as a bird finds itself without a partner, either as a current season juvenile, or as a widowed adult. Once formed, pair-bonds were stable with divorce and re-pairing virtually unknown.

It is likely, therefore, that the physiological demands of producing eggs, and the limitations of time available to rear two broods in a season, have influenced the course of sexual selection towards early mate

acquisition, stable pair bonds and a large investment in offspring by males early in the season.

The logical option of producing one large first clutch, as do most of the Paridae, must be considered. There is probably less fluctuation in food supply in New Zealand than in Northern Hemisphere countries. Consequently the Rifleman produces a clutch whose size is compatible with the food available for feeding nestlings later in the season. The concept of a clutch size commensurate with available food supplies has been supported by research on other species (eg Lack 1968).

7. The Laying Seasons of Other Endemic Passerines at Kowhai Bush

A. The Grey Warbler and Rifleman compared

Female Riflemen weighed on average 6.98g (SD = 0.60, n = 40), about half a gram more than female Grey Warblers ($\bar{X}$ = 6.44, SD = 0.50, n = 6, Gill 1980a). However, Gill's data are too few to test the difference statistically. Despite this, the female Rifleman's larger size could be important, for she lays significantly larger first clutches ($t = 5.08$, $P < 0.001$, $df = 143$).

The Grey Warblers' and Riflemen's modes of feeding may also be important in explaining the Grey Warblers' smaller first clutches. Riflemen are restricted to gleaning from the ground and all parts of the tree except the ends of green twigs. Gill (1980b) reports that 41% of the Grey Warbler's feeding time is spent hovering, taking invertebrates from green leafy twig ends which the Rifleman cannot exploit. Perhaps the invertebrates occupying these different niches become abundant at different times of the year. However, it would be necessary to record the abundance of invertebrates at different sites and precisely where the birds foraged to assess the importance of different feeding modes.

Another difference between the Grey Warbler and the Rifleman is that there is no courtship-feeding among Grey Warblers. The difference is difficult to explain considering that the female Grey Warblers lay about as frequently as the Riflemen do and lay eggs relatively as large with respect to female body weight. It appears that at least one biologically significant difference between these species lies in the Grey Warbler's smaller clutch size and this could remove the need for courtship-feeding. However, the final solution to this problem must include gauging the significance of other ecological variables such as their different feeding niches and time of laying and how these relate to food availability.

B. The Laying Season of the Rifleman compared with Robin, Brown Creeper and the Fantail

Courtship-feeding is a regular feature of behaviour among Brown Creepers and Robins during incubation. In these species only the female incubates. With Riflemen and Fantails, both sexes incubate and no courtship-feeding occurs during incubation. Grey Warblers cope without any courtship-feeding yet lay earlier than the other species except Robins. Furthermore, only the female Grey Warbler incubates.

Despite Grey Warblers laying earlier than Brown Creepers there is no significant difference between the average size of their first clutches (t test, $P > 0.05$; Appendix 2). Brown Creepers lay about three weeks later than the Grey Warblers but unlike Riflemen and Grey Warblers, Brown Creepers lay every 24-hours.

Robins lay earlier and significantly smaller first clutches than the other species (Fantails $t = 11.55$, $df = 240$, $P < 0.001$; Grey Warblers $t = 14.21$, $df = 137$, $P < 0.001$; Brown Creepers $t = 8.10$, $df = 120$, $P < 0.001$; Riflemen $t = 23.59$, $df = 204$, $P < 0.001$; Appendix 2). However, as has been pointed out, the relationship between date of laying and average clutch

size does not consistently apply to the other species.

The foraging techniques used by Robins, Grey Warblers and Fantails are described by Gill et. al. (1983). Robins are almost entirely ground foragers and can cache food for later use (Powlesland 1979). Courtship-feeding occurs among Robins probably to help in egg production. Gill et. al. (1983) postulate that ground-dwelling invertebrates become abundant before foliage dwellers (especially caterpillars) which in turn are more abundant than flying insects. They ascribe the following order of laying to changes in food availability: Robin, Grey Warbler and Fantail.

Gill (1980b) describes Grey Warblers as gleaners taking 94% of food items from twigs and living foliage. They employ their "hover-glean technique" 41% of the time. For most (55%) of the remaining time the Grey Warblers glean from the thin branchlets, twigs and live foliage while perching upright. Grey Warblers spend very little time gleaning from main branches or trunks as do Riflemen and Brown Creeper. The explanation for Grey Warblers laying earlier than Riflemen and Brown Creepers is more likely to include not only an earlier source of food at their preferred feeding locations, but also that they exploit a specific part of the substrate better than the other two species.

Observations of Riflemen and Brown Creepers show that neither of them could hover and forage as effectively as Grey Warblers. Riflemen have been seen attempting to hover but they seem completely unable to stay in the same position. Brown Creeper have not been seen hovering. Thus Grey Warblers exploit a particular feeding niche without interspecific competition which together with a possible earlier abundance of exploitable food, might advantage Grey Warblers over the others by allowing them to start laying sooner. That Riflemen and Brown Creepers lay about the same time is consistent with the above hypotheses since both these species are

restricted to gleaning.

Gill et. al. (1983) report that Fantails are entirely aerial feeders. Presumably a large proportion of the insects caught are adults which are not available in large enough numbers before early October when the bird's laying season starts. The more tenuous nature of the Fantail's food supply might also be important - numbers of flying insects must be more subject to fluctuation due to weather changes than non-airborne invertebrates. Consequently, adequate periods of fine weather are probably also important before Fantails can lay.

8. Other Considerations.

A. The Cost of Gonadal Development.

The calorific cost of testicular synthesis is less than 1 per cent of BMR (basal metabolic rate) (King 1972). It is clear that the main extra energetic cost to the male Rifleman during the pre-laying and egg-laying periods is courtship-feeding.

The amount of data available on the calorific cost of ovarian and oviductal recrudescence is limited (King 1972). However, King states that during the period of maximum growth rate "it can be an appreciable fraction of the female's energy budget, but less than 10 per cent of BMR". When growth rate is less than half the maximum acheived, King considered the calorific cost to be negligible.

Two important questions are: how long is the period during maximal growth, and does it occur during the courtship-feeding period? There is no information on Riflemen to answer these questions but it is presumed that the period of maximal growth is short and that it occurs when courtship-feeding is taking place. Thus it is not possible to assess accurately the significance of the female's outlay in energy for ovarian and oviductal development against the contribution of the male by

courtship-feeding. However, it seems likely that the outlay of energy on oviductal development is small as compared with the outlay of energy on eggs (Kendeigh 1941).

B. Albumen Formation.

King (1972) considered it likely that the pattern of energy requirements for the albumen formation of an egg would rise and fall in a sinusoidal fashion. The extra energy demands of albumen formation might also be part of the reason for the Rifleman having a long laying-interval as the albumen is laid down in the oviduct after ovulation.

9. CONCLUSIONS.

(1) During the pre-laying and laying periods the female Rifleman only gathers enough food for her maintenance requirements and the male supplies her extra needs for laying the first clutch.

(2) Courtship-feeding does not affect the efficiency of the female Rifleman's foraging.

(3) The benefits of courtship-feeding almost certainly include the supplying of essential elements, especially calcium, rather than simply meeting the calorific requirements of oogenesis.

(4) The period of the highest rate of courtship-feeding coincides with the period of nutrient and calorific demands on the female for oogenesis.

(5) A 48-hour laying interval helps reduce the maximum nutrient and calorific demands on the female during the laying period.

(6) The system of courtship-feeding and the organisation of a laying pair's time budget, suggests Riflemen maximise efficiency of effort as

evidenced by the birds staying together almost continuously and the virtual absence of ceremony during courtship-feeding.

(7) The importance of courtship-feeding reflects high male parental effort early in the season which supports the main hypothesis of the thesis which predicts a large amount of parental cooperation.

SECTION TWO : INCUBATION

A. INTRODUCTION

Incubation may be defined as the transfer of heat to the egg. Most birds achieve this by supplying body heat while "sitting" on the clutch. If there is a negative thermal gradient between the body core and the egg then heat will be lost from the incubating bird to the eggs. The manner in which a breeding pair partition their time on the nest can vary from one sex or the other doing all the incubating to a system where both sexes participate.

One of the most important questions regarding incubation is whether it involves any cost to the sitting bird. In answering this question it is helpful to list the possible costs and benefits to the bird of incubating behaviour. However, this approach may fail to identify all the relevant factors if these are assessed from the observer's point of view.

One cost incurred is the time spent on the nest which might otherwise be spent doing something else e.g. foraging or preening. This "opportunity" cost should be considered in addition to any extra outlay in energy needed to heat eggs. A diurnal bird incubating by day might need to increase its foraging rate to compensate for the time lost while incubating. However, this may be offset somewhat by the thermal insulation afforded by the nest. Also, as the breeding season advances, the number of daylight hours available for foraging, and possibly food availability, increases.

The consideration of possible costs to incubating birds becomes further complicated as it is possible that the returns from increased foraging are unlikely to be simply directly proportional to foraging effort. Consequently, there must be a point when the returns from a higher foraging rate cannot compensate for having more time available for foraging.

Foraging opportunity may be particularly important at the time of year when first clutch incubation occurs as food supply is unlikely to have reached a peak.

Other costs to incubating birds include the energy spent in flying between the nest and feeding areas. During incubation the sitting bird may be prone to predation, or it may increase its chances of being killed by a predator because of the regular pattern of its behaviour in flying to and from the nest.

The benefits accrued to the incubating bird are related to the thermal insulative properties of the nest. Walsberg and King (1978b, page 652) report that in the birds they have studied (two cupular nesting passerines) "the effect of the nest's microclimate and insulation more than compensate for heat loss through the brood patch". The benefits of insulation might be particularly significant in a hole nesting species such as the Rifleman. Any advantages of insulation that the nest affords must be greatest during the night when the coldest temperatures of the day are experienced.

The question of whether incubation costs energy is dealt with later. The controversy involved in energetic studies of incubation centre around whether incubating involves a net energy outlay from the incubating bird. The problem is made difficult because it is not possible to separate the extra heat (if any) of warming eggs from the normal heat produced from maintenance of the bird. In tackling this issue authors have measured different parameters to arrive at their conclusions.

Walsberg (1983) questioned the relevance of other workers' comparisons reasoning that the comparisons they made were not "ecologically relevant" and did not reflect the bird's behaviour in the wild. Examples given included open-flow gas analysis type studies such as Biebach's (1979) on Starlings (Sturnus vulgaris). The energy consumed by an incubating bird was determined from the volume of oxygen used and this was compared with

the energy consumed by a bird sitting voluntarily in a box without eggs. Biebach concluded that within 12-22°C the energy consumption was the same, that the warmth required for incubating was a side-product of normal metabolism and that no extra energy was required to incubate. As Starlings do not usually sit in nest boxes unless breeding, according to Walsberg, Biebach's control was invalid. Further, the technique of drawing air through the nest may increase energy expenditure by lowering air temperature and relative humidity within the nest cavity.

The cost of incubation can be measured using the increase in food consumed by an incubating bird. From his study on Zebra Finches (Poephila guttata) El Wailly (1966) concluded that incubation entailed an increase in energy expenditure. However, Walsberg discounted this conclusion because energy allocation to other activities such as foraging is often radically changed during incubation as compared with non-incubating birds. Because there was no measure of or control for the outlay of energy on different activities it was not possible to tell how much of the changes of food intake were due to egg thermo-regulation.

Finally, Kendeigh's (1963) biophysical model was criticised by Walsberg because it assumed that the measured heat flow from the incubating bird was additional to parental metabolism.

Walsberg and King (1978a) have used resting energy expenditure to compare energy use by a bird incubating and one perching in the same microclimate in which the nest is situated. Their comparison is adequate for the night time situation for some species where one bird incubates while the other roosts outside, as is the case with Riflemen. However, during the daytime the non-incubating bird is most likely involved in a more energetically costly task than perching so that this study does not enable an ecologically meaningful comparison either.

Other workers have been able to compare the daily energy expenditure of

incubating and non-incubating birds. The quantity DEE refers to the total amount of energy expended by the birds daily activities. Walsberg (1977) showed that incubating female Phainopepla nitens have a DEE which is 7% lower than non incubating females. Similarly, Mugaas [(1976) in Walsberg and King (1978b)] calculated that female Black-billed Magpies' (Pica pica hudsonii) DEE averaged 25-39% below that of non breeding females. According to Walsberg and King (1978b) the DEE of these two species reached the lowest annual level during incubation. The difference in the figures for these two examples correlates with two-sex and single-sex incubating systems respectively, although another factor responsible for this difference is the reduced time in flight.

Measuring DEE and comparing it between incubating and non-incubating birds is of limited use in deciding whether incubation costs the parent energetically because the value of DEE does not indicate the net amount of energy left to the bird (if any) after all the various outgoings on the daily energy intake have been taken into account. It seems, a priori, that the DEE of an incubating bird is almost certainly going to be less than a non-incubating bird or one that does less incubating because it is involved in less active behaviour such as flying.

Vleck (1981) compared the metabolism of two adult Zebra Finches whilst in the nest. The metabolic rate of the bird incubating eggs was 20-23% above that of the nonincubating birds resting in the nest. As stated earlier, Walsberg (1983) criticised the results of the workers using biophysical models because they assumed that the measured heat flow was additive to parental metabolism. If Walsberg's argument is correct then Vleck's results should not show any difference between the incubating and non-incubating birds. Instead, Vleck found an increased loss of energy which implies that while the bird is on the nest a proportion of its

productive energy is being used to heat the eggs. In order to calculate this proportion it would be necessary to calculate the energy budget for the bird, including productive energy, and the amount of energy outlaid in incubation.

It is agreed that Vleck did not use an ecologically meaningful control given that non-incubators in the nest do not occur naturally. However, non-breeding Zebra Finches in the wild do sometimes roost in breeding nests (J.Warham pers. comm.). At least Vleck's results serve to show that incubation does use energy additional to the parent's metabolism. Heat lost normally to the environment is no doubt important for heating eggs but is not always adequate for normal embryo development.

What remains undetermined in this argument is what is the relative contribution to heating the eggs from (i) energy normally lost to the environment and (ii) additional energy that the bird has to supply which might otherwise have been used for somatic growth, maintenance etc. The latter component could be termed "productive energy" used in incubation because it is energy that would be included in "production" in the widely used formula representing the total energy budget of an animal:

$$C = P + R + F$$

where C = total energy used P = energy used in production ie. somatic growth and gametes, R = energy lost to the environment due to respiration and F = energy lost as faeces. The component of "normal heat loss to the environment" in the total amount of heat passed to the eggs (measured in the above mentioned biophysical studies) has not been considered in calculating the proportion of productive energy used in incubation.

Assessing the tax on productive energy of incubating is the best index of the cost to the parent because, when compared with another's activity budget, this figure takes into account all the costs and benefits of each individual's time-activity budget. The productive energy available to the

non-incubator or partner incubating least might well be more than to the bird incubating most. A greater availability of productive energy could be expected if the extra time was spent on foraging where the net gain in energy is likely to be more than for a bird sitting in a nest.

In this study, it is assumed that incubating incurs parental cost as productive energy, although part of the energy used to heat eggs would have been lost to the environment anyway. Measuring the amount of productive energy used in incubating was technically beyond the means of this study. Instead, the attentive behaviour of the parents on the nest was measured and is used as an index of parental effort.

Biophysical aspects of incubation:

The proportion of productive energy used during incubation was calculated for the House Wren (Troglogytes aedon) by Kendeigh (1963). He determined that the "average percentage of the total potential productive energy needed for incubation varied from 17% at an air temperature of 22.3°C to 51% at 17°C"(page 903). His findings illustrate how the eggs act as a heat sink, the size of which varies with the size of the thermal gradient between the inside of the eggs and the ambient air temperature. The principal factor governing the maintenance of egg temperature is the cooling rate of eggs which is in part modulated by the thermal insulative properties of the nest and the behaviour of the incubating bird.

The rate and degree of heating by the incubating bird is achieved by what White and Kinney (1974) term "tightness of sit". Incubating Riflemen and other species in Kowhai Bush have been observed modifying the way they sit over the eggs. Presumably they are varying the degree of contact of the brood patch with the eggs and thereby regulating the amount of heat passing to the eggs.

Hypotheses about Rifleman incubation:

In considering the incubating system of a species it is important to take into account the pattern of parental care in the foregoing periods of the breeding cycle. With second clutch incubation by Riflemen, parents had to cope with feeding dependent offspring while incubating concurrently. The hypothesis tested in this study was that during first and second clutch incubation, the pattern of parental care favoured the female energetically because of the prior demands of egglaying and the concurrent demands of feeding juveniles while incubating second clutches.

Hypothesis: that the males undertook most of the first clutch incubation.

At night, the situation was likely to be reversed because the bird roosting outside would have none of the thermal insulative benefits of the nest.

Hypothesis: that females undertook all of the incubating at night.

During incubation of the second clutch, consideration of the other parental demands was necessary to make predictions about parental care. While the second clutch was incubated, juveniles from the first clutch had to be fed. The feeding of young is the most demanding phase of breeding in most nidicolous species of birds (Ricklefs 1974). The demands of egglaying and of feeding fledglings during the incubation of second clutches probably influenced incubation.

Hypotheses: (i) that females would spend more time incubating than males in the early stages of second clutch incubation when the fledglings were more dependant.

(ii) that the males undertook most of the feeding of young.

The latter hypothesis is tested in section three. That females undertook the least costly type of parental care would by expected if the

main hypothesis that a large proportion of parental effort was undertaken by the male is correct. Another outcome of this hypothesis is that the male would do most of the incubation during the colder periods of the day such as early morning and late evening. Finally, the demands of incubation might have been alleviated for both parents if the nest was designed to maximise thermal insulation. The structure of the nest was investigated with this in mind.

B. METHODS

1. Field Observations:

In order to sample parental care systematically it was essential to know at what stage of the breeding cycle a pair had reached on any given day. Thus daily checks were made on all nests during the laying period. Hides were set up at most of the nests used. Those at which hides were not used all belonged to unbanded birds from the first season's work. These birds showed no outward appearance of reacting to observer presence unlike banded birds of subsequent years. Little information from these nests was used in the analysis.

After the first season most birds observed were banded which, coupled with their obvious plumage sexual dimorphism, made identification of individuals entering and leaving the nest relatively easy. The time birds spent sitting was measured using a stop watch and data were recorded on a portable Sony tape recorder.

2. Sampling:

The incubation period was divided into five intervals of four days. The mean length of incubation was 19.7 days ($n = 80$ nests, $SD = 0.8$). The

daylight hours were divided into three equal periods. For any nest under observation the object was to obtain one hours observation for each day-period within each interval of incubation. Nests were watched for one hour spells in order to observe at least two sitting spells per parent.

A period of ten minutes or so was allowed to elapse before recording data if the observer was seen entering the hide by the birds. Usually the birds were quick to settle down after any disturbance.

3. Empirical information collected

(i) the length of time parents spent in the nest - a bird "sitting" in the nest was presumed to be incubating.

(ii) the number of visits in which incubation occured.

(iii) the number of visits to the perch

(iv) the number of visits to the nest box's perch - termed inspection visits

(v) the number of feathers taken into and out of the nest

Weather conditions at the time of each sample were recorded by the observer and by a hygrothermograph as described in the general methods.

4. Night-time Observation Methods

Parental care of eggs at night was investigated by watching nests through the transition from full daylight until complete darkness and by spot-checking nests at night. On the four occasions nests were watched at night a 25 watt 12V neon ultra violet light run off a battery was used to illuminate the nest entrance.

Another technique involved making spot-checks on as many different nests as possible during the night. The identity of the incubating bird was determined by recognising the sexually dimorphic plumage using a 5mm diameter anuscope. The anuscope often gave a clear enough view into the

nest to ensure only one bird was inside.

5. Nest Air Temperature

Time calibrated temperatures recorded on a Grant's thermograph (see General Methods) indicated when the birds were on and off the nest, especially during the egglaying period.

C. RESULTS

1. Natural history of incubation by Riflemen

A. Nest sites and structure: Riflemen usually nested in a completely enclosed cavity with a small (11-30mm) opening to the outside. Usually the cavity in which the nest was built was situated in a solid site such as the hollow in dead or dying timber. In four instances Riflemen were found nesting underground. Two of these sites were old Rabbit burrows. Four more nests were found amongst the dense dead elongate leaves that gather under the crown of Cabbage Trees (Cordyline australis).

The structure of the nest gave efficient thermal insulation. The male and female first built a base about 20mm thick of coarse material e.g. small twigs. The next stage involved building the super-structure of the bowl of the nest. The base was built up into a bowl and gradually closed in. The material used was finer and longer than that used in the base. At this point the grass stems were interwoven as if they had been spun to form a sphere. When the sphere enclosing the cavity had been made, it was thickened by adding to it from the inside using finer building materials such as grass or leaf skeletons. Next a tunnel about 25mm in diameter was woven into the structure. The orientation of the tunnel was usually off-centre from the cavity entrance and the tunnel itself opened above the floor of the nest bowl. The woven sections of the nest were extremely tight-knit and tidy in appearance. After the main structure of the nest was finished a lining of coarse feathers was placed around the entire bowl. These feathers were generally primary or secondary feathers of other birds collected from within the territory. Another, less uniform, layer of down or soft feathers was now added. Although this basic structure was typical the actual materials used varied according to the common plants growing in

the vicinity of the nest site. The diameter of the bowl cavity was about 35mm and the thickness of the nest wall from the top into the bowl cavity was usually 15mm to 25mm.

B. Behavioural characteristics: The feather lining of the nest apparently improved thermal insulation. During the laying period, before the onset of incubation, Riflemen often left the eggs covered with downy feathers. Eggs were sometimes covered when birds left the nest during incubation. The entrance of the nest was often blocked with downy feathers during incubation when the nest was left in cold weather and when incubating at night.

During incubation, nesting material tended to become slightly damp due to condensation from the birds occupying the nest, and to water leaking into the box. This problem was alleviated by parents taking out wet feathers and drying them by teasing them out on a perch or by discarding them and replacing with new dry feathers.

Both sexes of the Riflemen had brood patches on the ventral surface in between the sterno-abdominal feather tracts during incubation and at least the first few days of the nestling period.

C. Differences between first and second clutch nests: Most first clutches were incubated during October; second clutches were incubated in late November and early December. The average ambient air temperatures during these periods were 9.8°C and 12.9°C respectively. First clutch nests weighed significantly more than second clutch nests (first clutch $\bar{X}$ = 40.5g, SD = 6.7, N = 124; second clutch $\bar{X}$ = 37.6g, SD = 6.7, N = 46; U test U = 3463.5, Z = 2.14, P = 0.02) suggesting that poorer nests were built when temperatures were higher. The nests used for these measurements were all taken from boxes with the same internal dimensions. Second clutch nests

were usually less well formed than first clutch nests, with thinner walls and less copious feather linings.

2. Empirical Results

A. Weather conditions over sampling

Observations were made regardless of weather conditions and, therefore, under all weather conditions experienced by Riflemen. Weather conditions did not impair the observer's abilities and most observations were made in equable conditions (Table 1).

Table 1 Weather conditions during sampling

A. First clutch incubation				
Variable	Scale			
	0	1	2	3
wind	128	60	23	7
temperature	64	108	40	6
cloud cover	78	79	39	22
B. Second clutch incubation				
wind	73	42	22	11
temperature	36	78	29	5
cloud	43	64	35	6

B. Sample size, season and number of pairs observed

Incubation was observed for periods of one hour - subsequently termed "watches". Riflemen were observed incubating for three seasons over first and second clutch incubation for 218 and 153 hours respectively (Table 2).

Table 2 Occasions incubation was observed each summer

	1980/81	1981/82	1982/83	Total
A. First clutch	34	120	64	218
B. Second clutch	15	55	83	153
Totals	49	175	147	371

Although up to 16 different pairs were observed in any interval, approximately two thirds of the observations during the first and second clutch incubation periods were about equally divided among five different pairs (Table 3).

Table 3 Different pairs and nests watched during incubation (both study areas)

A. First clutch	Day interval					
	1-4	5-8	9-12	13-16	17-21	Total
number of nests	8	9	16	15	11	23
number of pairs	7	7	12	12	10	16
B. Second clutch						
number of nests	6	7	9	8	11	11
number of pairs	5	6	8	7	11	10

The number of different nests watched is usually different from the number of pairs watched because some pairs were observed during the course of two or more seasons. When the sampling distribution between different pairs is broken down by four-day intervals and by three periods during the day at least five different pairs were observed (Table 4). The three periods during the day represent the original six periods during the day grouped into three : periods 1 and 2 = 1 ; periods 3 and 4 = 2 ; periods 5 and 6 = 3. This grouping is used throughout the rest of the thesis.

Table 4 Different nests and birds sampled during (A) First and (B) Second clutch incubation

A. Four-day intervals of incubation

	1–4			5–8			9–12			13–16			17–21		
var	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
1	13	5	3	13	7	3	18	10	3	11	7	3	19	8	3
2	9	5	3	13	5	3	15	11	3	21	11	3	24	10	3
3	11	5	2	11	6	2	19	9	3	13	10	3	15	6	3
B.															
1	8	4	2	9	5	3	6	4	2	10	6	3	13	7	2
2	10	5	2	10	6	2	13	8	3	11	6	2	14	7	3
3	7	4	2	9	5	3	14	7	3	12	5	2	6	4	2

Key for columns and rows:
var a = number of times nests were watched
b = number of different pairs sampled
c = number of different seasons over which sampling occurred
1 = first one third of daylight hours
2 = second one third of daylight hours
3 = third one third of daylight hours

C. Ambient temperature and attentiveness:

Attentiveness may be calculated by dividing the total time spent in the nest box by the time spent watching the nest. This ratio is usually presented as a percentage.

Correlation analysis was carried out in two parts during incubation to allow for the possible influence of embryo thermogenesis on parental behaviour. The extra heat produced by the embryo could have reduced the time required of parents incubating. Except for the first 11 days of first clutch incubation there was a significant correlation between combined parental attentiveness and ambient air temperature (Table 5).

Table 5 : Spearman Rank Correlation Coefficients for attentiveness with ambient air temperature

Interval of incubation	Rho	N	t	
a. First clutch				
days 1-11	-0.12	84	-1.09	NS
days 12-21	-0.32	83	-3.04	P < .005
b. Second clutch				
days 1-11	-0.44	72	-4.09	P < .005
days 12-21	-0.54	62	-4.88	P < .005

The non-significant result during the first half of first clutch incubation could have arisen because (i) either both parents' or one parent's attentiveness was not affected by temperature or (ii) the ambient air temperature did not vary enough to influence parental attentiveness. Both of these options may have been true because (i) there was no significant correlation of either parent's attentiveness and ambient air temperature (Table 6) and (ii) an F test on the variance of ambient temperatures for the hours nests were watched in the first and second halves of the first clutch incubation period was not significant ($F = 1.28$, $df1 = 81$, $df2 = 81$, $P > 0.05$). However, the average ambient air temperature during which parental attentiveness was sampled over the first eleven days of incubation was significantly lower than for the last ten days (t test, $t = 3.26$, $df = 162$, $P < 0.05$).

Table 6 : Spearman Rank Correlation analysis relating parental attentiveness and ambient air temperature in the first eleven days of first clutch incubation

	N	Rho	t	
Male parent	86	-0.17	-1.58	NS
Female parent	82	+0.37	+0.37	NS

D. Partition of Work

(i) First and Second Clutch Attentiveness

Male parents undertook most of the incubation (Figure 2-1). During incubation of the first clutch males and females showed a variation in

attentiveness of only 2% and 1% respectively from one four-day interval to another. Parental attentiveness was highest at each end of the day (periods one and two) during second clutch incubation. The difference between these and the middle day period was 5% and 6% for males and females respectively and represents only an average fall and rise of less than four minutes per hour between periods one and two, and two and three, in either parent's attentiveness. The greater variation in attentiveness between periods during the day in second clutches was correlated with higher average ambient air temperatures (Table 7).

Table 7 Ambient air temperatures during the incubation periods

	First clutch			Second clutches		
Period in day	1	2	3	1	2	3
X	10.5	14.5	13.0	14.0	17.0	14.9
SD	4.5	4.0	4.0	3.0	4.7	3.9
N	61	55	50	43	26	37

The average temperatures for each period during the day in the second clutch were significantly higher than temperatures in corresponding periods during first clutch incubation (Table 8).

Table 8 : Comparison of averages of ambient temperature between first and second clutches

Interval of day	t	df	
1	4.44	102	P < .05
2	4.36	101	P < .05
3	6.43	94	P < .05

The medians shown in Figure 2-1 are similar to the overall median attentiveness and 95% confidence intervals calculated for the whole of incubation (Table 9). The 95% confidence intervals here and elsewhere in the thesis have been calculated using the method in Snedecor and Cochran (1980, page 136-137).

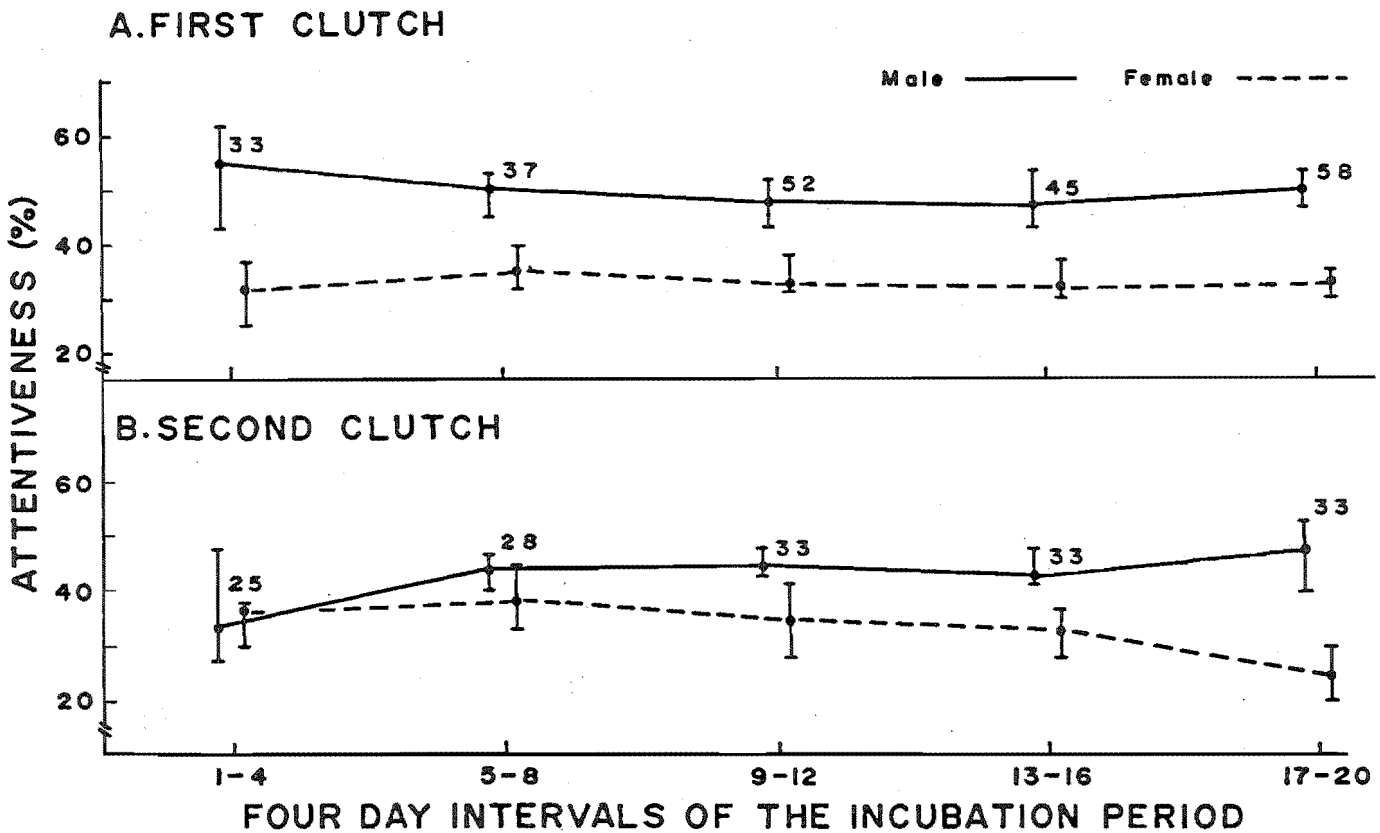


Figure 2-1 Proportions of time spent incubating by Riflemen parents over the incubation period (medians, 95% confidence intervals, sample sizes indicated).

Table 9 : Median attentiveness during incubation

	Male	95% CI	Female	95% CI	N
First clutch	0.48	0.47-0.52	0.33	0.32-0.35	225
Second clutch	0.45	0.42-0.47	0.33	0.30-0.35	152

Except in the first eight days of second clutch incubation the male spent about 1/3 to 1/2 more time on the nest during the day than the female did. The pattern of attentiveness generally varied little over incubation except during the first half of second clutch incubation. During the first four days the male's attentiveness was 10-14% less than that of the rest of the second clutch incubation period and the female initially spent 3% more time on the nest than her partner. The male increased its attentiveness from days five to eight by which time it spent 5% more time on the nest than the female. By days 9-12 a pattern similar to that in the first clutch had re-established itself whereby the male spent 9-13% more time on the nest than the female.

The male consistently reduced the time spent incubating in the second clutch relative to the first clutches, the difference being greatest in the first four days (22%), while the female increased the time spent on the nest with the second clutch by 1-4% except in the last four days during which she reduced her time by 8% (Table 10).

Table 10 : Median attentiveness (%) of parents during first and second clutches

Four-Day Int.	1-4		5-8		9-12		13-16		17-20	
	M	F	M	F	M	F	M	F	M	F
First clutch	55	32	50	35	48	32	47	32	50	33
Second clutch	33	36	44	39	45	35	43	33	48	25
Change	-22	+4	-6	+4	-3	+3	-4	+1	-2	-8

The relatively greater time spent on the nest by males made extra time available to females for other activities. During the time of year when first and second clutch incubation occurs, the number of hours of daylight was calculated from sunrise and sunset data supplied by the Meteorological Service plus one hour for the half light at each end of the day when Riflemen were active. The number of daylight hours during the first and second clutches were approximately 14 and 16 respectively. Thus, if males spent 15% and 12% more time on the nest than females during first and second clutch incubation, this left females with about two hours to do other things.

(ii) Results of Wilcoxon Matched Pairs Sign Rank Test on Parental Attentiveness:

The total time on the nest for males and females was measured each time incubation was observed. Except in two cases, the males spent significantly longer on the nest than females while incubating first clutches (Table 11). However, there was no significant difference during the first half of second clutch incubation until days 9 to 12, when the male sat significantly longer than the female.

Table 11 : Wilcoxon Matched Pairs Sign Rank Test (1-tailed) on the time males and females sat during incubation (statistic, probability)

A. First Clutch

Interval in day	Four-day interval of incubation 1 - 4	5 - 8	9 - 12	13 - 16	17 - 20
1	12, P <.05	7, P<.002	11, P<.006	11, P<.025	3, P<.001
2	14, P >.05	12, P<.008	16, P<.005	20, P<.003	34, P<.002
3	1, P <.002	18, P> .05	24, P<.003	11, P<.005	6, P<.001
B. Second Clutch					
1	8, P >.05	18, P >.05	2, P >.05	8, P <.05	7, P<.005
2	22, P >.05	13, P >.05	7, P<.002	13, P <.05	11, P<.005
3	7, P >.05	15, P >.05	20, P<.003	13, P <.02	0, P<.02

(iii) Nest Visits

The number of visits to the nest was recorded as one of five types: arrival at the nest entrance; flying to the nest entrance and peering inside for up to 30 seconds; entering the nest and leaving again; entering the nest with a feather which was deposited; sitting in the nest incubating eggs.

The first three types of visits were so infrequent that for most occasions when incubation was watched they were scored as zero. Hence, in Table 12 the frequencies of these visits are grouped. Even with grouping there were many zero values and so the standard deviations of mean hourly visits were not calculated. A similar situation occurred with the number of feather visits and again standard deviations were not included. In Table 12 the data for each period during the day have been grouped. There was no significant difference in the average frequency of sitting visits between parents in the first clutch except during days 9-12, when males made significantly more visits than females (t test; t = 6.10, df = 102, P

< 0.05). In days 17-20 of the second clutch the females made on average significantly more sitting visits per hour than the males (t test; t = 19.92, df = 64, P < 0.025). Otherwise during the second clutch there was no significant difference in the number of sitting visits.

Table 12:Average frequency of visits per hour during incubation

A.First Clutch

	Day Interval of Incubation														
	1 - 4			5 - 8			9 - 12			13 - 16			17 - 20		
	M	F	N	M	F	N	M	F	N	M	F	N	M	F	N
Visit type :															
non-inc.	1	.2	33	.6	.2	37	1	.4	52	.5	.4	45	1	.5	58
feather	.2	.1	33	.2	.1	37	.5	.2	52	.3	.2	45	.4	.3	58
incubating	3	5	33	2	2	37	3	2	52	2	2	45	3	2	58
+std.dev.	1	4		.7	.9		2	.7		1	1		.7	.7	

B.Second Clutch-

Visit type :															
non-inc.	2	0	25	.5	.1	28	1	.5	33	.5	.2	33	.8	.9	33
feather	2	0	25	.5	.1	28	.7	.3	33	.1	.1	33	.6	.4	33
incubate	3	5	25	3	2	28	3	2	33	5	8	33	3	5	33
+std.dev.	1	3		1	1		1	1		3	6		1	.4	

Males deposited significantly more feathers in the nest than females (Chi Square tests for each clutch, P < 0.05, Table 13).

Table 13 : Feathers taken into the nest during incubation

	Male	Female	X^2	df	P
A.First Clutch number of feathers	80	42	5.21	1	<0.05
B.Second Clutch number of feathers	105	29	n	1	<0.05

(iv) Parental Care at Night

Only the female roosts in the nest during the night. One nest was watched three times and another once. On each occasion only the female had remained after night-fall. Twice the male was seen roosting in the tree

above the nest box. Thirty one spot checks were made on eight different nests between 1900 and 2200 hours over two seasons. On each check the female was sitting alone. Feathers were observed blocking the nest entrance four times.

D. DISCUSSION

1.The Rifleman incubation system

The two most important features of the Rifleman's incubation system were (i) the means by which the birds have minimised the thermodynamic problems of heating such a relatively large mass of eggs, and (ii) the cooperative biparental care of eggs which favoured the female in terms of energetic cost.

The first clutches of five eggs laid by Riflemen weighed approximately the same as an average female and about 120% of an average male Rifleman's body weight. This proportionately large mass of eggs was probably kept at about 35°C which is the temperature required for embryo development in passerines (Kendeigh 1963). The incubation behaviour of the Rifleman, therefore, must be a consequence of minimising the energetic demands of a small bird keeping large eggs warm. If the parents are to maintain 35°C continuously, any drop in average ambient air temperature will require more time on the nest and an increasing proportion of foraging time. However, there must be a point at which low environmental temperatures impose a limit on the time resources of a bird and its ability to breed. The latter constraint includes the time which eggs are left exposed after the departure of the parent.

According to Kendeigh (1963) the rate of cooling of the eggs exceeds the rate of heating after the parent returns. Hence, the time required to return eggs to normal temperature exceeds the length of absence. Consequently, the parents are energetically penalised for every absence.

This is because returning the embryo to normal development temperature costs energy, and until the embryo is again metabolising normally, there is no return on that energy expenditure.

Biparental care is the most widespread and primitive form of parental care in Class Aves (Drent 1972; Skutch 1957). However, amongst passerines the female typically undertakes most, if not all, incubation (Skutch 1957). In Riflemen this pattern is reversed.

During the care of the first clutch the male incubated about half as much again as the female. Assuming that Riflemen embryos required a minimum combined parent attentiveness of 81% (the observed total attentiveness) during the first clutch incubation, it seemed unlikely the female could have coped with supplying all or the bulk of attentiveness. Jones and Ward (1976) showed that the female Red-billed Quelea (Quelea quelea) suffered a drop in intra-muscular protein reserves over egglaying which was recouped during the incubation period. The female Rifleman was probably in a similar situation after laying where it needed to regain lost reserves. The greater amount of time spent incubating by the male allowed the female about two hours more foraging time per day, perhaps because of her need to regain condition after laying her relatively large clutches.

The drop in male attentiveness over the first eight days of the second clutch as compared the same period during first clutch, was most probably due to the male having to cope with the energetically more expensive burden of feeding first clutch fledglings (Ricklefs 1974). During the first eight days fledglings were still largely dependant on the parents. Most of this feeding of fledglings was carried out by the male (see section 3). Despite the female spending more time on the nest over the first four days of the incubation of second clutches, her attentiveness at any time did not differ markedly from the first clutch. Some of the change in total attentiveness might have been due to higher ambient air temperatures.

However, this was unlikely to account for all of the difference as the combined attentiveness over the whole of the second clutch was only 3% less than the first clutch.

By the eighth day of incubation, the first clutch fledglings were largely independent and the male resumed its principal role of incubating the second clutch. For the female's part, the smaller contribution feeding the fledglings and the unchanged attentiveness is probably due to needing to recoup after the energy demands of laying the second clutch (on average about 72% of her body weight), unaided this time by courtship-feeding (Section 1). Egglaying must have required an extra commitment of time for foraging above maintenance needs and the demands of fledglings. Further, some time and energy for nest building was required as both parents built the second-clutch nest.

During the transition from the end of the first clutch nestling period into second clutch incubation there occurred the greatest number of different but simultaneous demands on the birds. The observed patterns reflected a high degree of parental cooperation to enable the birds to rear a second brood. The importance of the male in the incubating system was exemplified by the presence of a brood patch in males which remained for the duration of brooding the nestlings. According to Skutch (1957) in passerines there is a lack of correlation between male incubating behaviour and the presence of a brood patch. Considering the male Rifleman's role in incubation and the size of the clutch, the brood patch was necessary for the bird to act as an efficient heat shunt.

In assessing the energetic cost of incubation to the parents any contribution of the embryo in maintaining egg temperature should increase throughout the incubation period as the embryo matured. Any benefit should be the same for each parent and is unlikely to have changed any conclusions.

Night-time parental care during incubation also seemed to favour the female as the male roosted outside and the female stayed inside the nest as shown by Walsberg and King (1978a) for Mountain White Crowned Sparrows (Zonotrichia leucophrys Oriantha). These authors showed that the resting energy expenditure of an incubating bird was 15% lower than for one not incubating and exposed to the same microclimate. Thus, these results yield an ecologically meaningful comparison because both sparrows are usually passive during the night-time and only one bird occupies the nest as occurs with the Rifleman. Hence, Rifleman incubation behaviour at night was consistent with the hypothesis that the female required the most favourable partition of parental care to recover from egglaying by roosting inside the nest.

Despite the clear results of Walsberg and King (1978a) regarding energy expenditure during night-time incubation, the situation is not so clear in at least one other study. Mertens (1980) found, using heat flux transducers, that heat production by incubating female Great Tits' (Parus major) was two to four times BMR and that the non-incubating bird roosting outside required only basal energy expenditure. However, according to Walsberg (1983) these results were higher than Merten's other published results using measurements of oxygen consumption and based on a biophysical model.

In the case of the Rifleman, the highly structured nest and its thermal insulative function, together with the results of other research which has measured energy expenditure during incubation at night, seems to indicate that Merten's results are in some way exceptional. Indeed, they were based only on one bird incubating nine eggs (about 100% of the female's body weight). Also, the Great Tit's nest is not fully enclosed as it is with the Rifleman and, therefore, is not likely to be as well insulated.

Apart from the change from biparental care during the daytime to female parental care at night, there were no obvious changes in the pattern of incubation between the three sampling periods during the day. However, there was a significant negative correlation between ambient air temperature and parent attentiveness during daylight hours, indicating that incubation behaviour was sensitive to the main environmental factor likely to affect the embryo's temperature. The only time this relationship did not hold was during the first half of the first clutch incubation. During this period, ambient air temperature was significantly lower than in the second half. The lack of correlation could have been because the range of temperatures experienced were too low to allow any alteration of the time spent incubating for adequate embryo development.

2. Other costs during incubating:

Male passerines generally do not have brood patches (Skutch 1957). The brood patch's function is to bring heat to the skin surface efficiently (Ricklefs 1974) and is achieved because of increased vascularisation and blood flow. That the male Rifleman plays such an important role in the incubation of the eggs is consistent with their having a brood patch. It was assumed the cost of developing a brood patch and any re-feathering after was the same for males and females. The cost may be minimal anyway (Ricklefs 1974).

Other costs to incubating birds included the energy outlaid flying between the nest and feeding areas and the risk of predation. The former may not have been a significant consideration in determining relative parental energy outlay by Riflemen because there was no significant difference between the number of visits per hour for males and females. Two nests were preyed on during incubation and the females incubating disappeared. Although the risk of predation is a potential cost to the

incubating parent, and perhaps more so for the female because she sits at night, the risk seems small given the low incidence of predation during incubation and the inaccessibility to predators of hole nests.

3. Rifleman incubation behaviour as compared with other Kowhai Bush passerines:

A relationship exists between the length of incubation period and relative clutch size (Rahn and Ar 1974) but does not occur with the native passerines studied at Kowhai Bush (Appendix 2). Riflemen were notable for their exceptionally long incubation period which averaged 19.6 days. The Brown Creeper has an incubation period of 19-21 days (Cunningham, pers comm) yet it's average relative first clutch weight to female body weight is 67% as compared to 72% and 85% for Grey Warblers and Riflemen respectively. This inconsistency cannot be explained by the fact that the Brown Creeper is a cupular nesting bird whereas the Grey Warbler and the Rifleman have enclosed and hole nests respectively.

The lessened thermal insularity of the Brown Creeper cup nest might have accounted for their taking longer to incubate despite the smaller size of their clutch. However, the Fantail's clutch is about the same proportional and numerical size as the Brown Creeper's and is incubated in a cupular nest as well. Fantails on average take only 14 days to incubate and their eggs are a similar size (Appendix 2). It appears that resolving this problem requires consideration of other factors.

4. The Natural history of Rifleman incubation:

The progressively finer materials used towards the centre of the nest apparently improved thermal insulation and hence minimised the cooling rate of eggs. The latter variable is most significant in influencing egg temperature (Ricklefs 1974). Off-centred nest entrances that faced away

from the cavity entrance might well have been so arranged to reduce drafts and the loss of warm air. By situating nests in dead wood, Rifleman benefitted from it's excellent thermal insulation.

Riflemen used behavioural devices to reduce the cooling rate of eggs during incubation. One of these was to reduce the length of inattentive intervals. This was of particular value to the relieving bird because of the extra energy required to raise egg temperature again. For example, in the House Wren the difference in the cooling and heating coefficients of eggs meant that it took 1.6 times as long to heat an egg up to a temperature as it took for the egg temperature to fall below that level (Kendeigh 1963). If the change-over between incubating birds were acheived quickly, any drops in egg temperature would have been minimised because the eggs were not given the time to cool. Riflemen effected this by waiting for a specific call from the relieving bird before leaving. However, although this was the usual routine, it was not always the rule, especially during hot weather. The Rifleman's habit of covering eggs with feathers on leaving the nest must also have reduced the cooling rate of eggs.

Feather additions were uaually done by the male probably to maintain the thermal insularity of the nest. Many nests tended to become damp with condensation which could have seriously impaired their heat-retentive properties. The Rifleman's habit of removing wet feathers and drying them by teasing them out on a perch was also noted by Stead (1932) with the hole-nesting confamilial, Stead's Wren (Xenicus variablis).

Feathers were used to partially block off the nest entrance during night-time incubation, thereby improving thermal insulation by reducing air flow in and out of the nest. The feathers used in blocking the entrance and relining the nests were the soft and downy type which were best suited for insulation.

4. SUMMARY AND CONCLUSIONS

Kendeigh (1973 page 319) described nesting behaviour of birds as "conditioned to a very large extent by energetics as demonstrated by incubation costs, nest insulation, nest location, ambient temperature, season and geographic location". Drent (1973) supported this view and hypothesised an upper limit of the cost of incubation as 25% of productive energy. Despite the controversy over this question of "cost" the most relevant studies which have tackled the energetic issue have concluded that incubation requires some fraction of productive energy and, therefore, does cost the incubating bird in the broader sense.

The main conclusion from research to date is that the fraction of productive energy required is a function of the duration of nest visitation of each parent which in turn reflects a compromise between nutritional demands and egg cooling. The female Rifleman's nutritional demands must be greater than the male's because of egglaying and her larger body size. These demands are exceptionally high as evidenced by the relatively small mass of the female to the clutch. Therefore, one would expect the Rifleman's highly cooperative parental care system during incubation, which favoured the female and compensated for her energetic outlay in egglaying.

For a small passerine such as the Rifleman that breeds in low latitudes during periods of cold weather, one would expect behavioural devices which minimised the cost of incubation. The following conclusions have been made on the basis of this study and published results of other studies:

Conclusions

(1) The incubation system of the Rifleman is organised towards minimising the energetic demands on the female parent because of the need to rec uperate after egglaying.

(2) The male Rifleman performs most incubation during the day to allow the female extra time for foraging and to regain condition after the demands of egglaying.

(3) During the early part of incubating second clutches parental behaviour is a "trade-off" between differently costed parental obligations towards two concurrent nesting efforts of the first and second clutches.

(4) Rifleman parental care behaviour is consistent with the main hypothesis that energetic constraints on parents are minimised by parental cooperativity in the form of a high degree of male parental care.

SECTION THREE : PARENTAL AND NON-PARENTAL CARE OF YOUNG

A. INTRODUCTION

Few studies have been able to measure directly reproductive effort of particular activities in wild birds. Most studies have used indices of basal metabolic rate worked out in laboratory conditions to estimate the "energetic cost" of the time spent in various forms of parental care. In one study (Verner 1965), found that rearing young was energetically the most demanding period in the breeding cycle. Another study (Hails and Bryant 1979) calculated directly the average daily metabolic rate (ADMR) of House Martins raising young at first and second clutch nests. ADMR was equated to the amount of deuterium used over the nestling period. This value represents all the energy expended on all activity over the nestling period. The study showed that ADMR was related to the frequency of feeding nestlings since the calculated energy cost per feeding visit was similar for the smallest to the largest size of broods studied. The increased amount of work involved in feeding larger broods was done by the male.

Alternative ways of measuring reproductive effort have used survival and fecundity (Ricklefs 1977). For example, Askenmo's (1979) study on the annual survival of male Pied Flycatcher parents after raising artificially enlarged broods (which required more effort to rear) showed that increased reproductive effort was negatively correlated with life expectancy. Askenmo's study assumed that stresses involved in increasing the feeding rate to the young were responsible for the reduced life expectancy of the parent. Askenmo pointed out that the extra effort could have influenced future life expectancy by delaying emigration while the bird recovered from an abnormally low post-reproductive weight.

Other studies measuring daily energy expenditure (DEE) of birds showed

that DEE reached the highest seasonal value while feeding young, typically being 10-45% above that expended during incubation (Walsberg 1983). Walsberg states (page 180) that changes in power consumption result from behavioural changes rather than from "other factors, such as variation in the thermostatic requirement...behavioural plasticity, both proximate and evolutionary, appears to be a major determinant of phasic and interspecific variation of DEE".

Feeding typical nidicolous broods may be a greater strain on small-bodied than large bodied species (Walsberg 1983). This is because adult energy expenditure scales with body mass by a higher factor than do nestling requirements scaled with parental body mass. Thus "the proportional increase in rates of parental food acquisition associated with feeding a single nestling should decrease with an increase in body mass"(Walsberg, page 184). These considerations suggest that a small altricial passerine with nidicolous young such as the Rifleman would benefit by adopting a parental care system that minimised the energetic demands of feeding young. During the nestling and post fledging periods, therefore, the highest degree of parental cooperation should occur, reflected in a relatively high level of male parental effort.

In this study, "feeding rate" has been used as the main measure of parental and non parental effort (and consequently parental investment) as it is generally accepted as the single most energetically expensive activity in the breeding season. Other variables including non-feeding visits to the nest and brooding were measured and compared. If Riflemen employed a highly cooperative parental care system then it was expected that the male parent contributed significantly to the care of young. The following hypotheses were set up to test whether male Riflemen parents were important in cooperating in the parental care of young:

(1) That the male parent undertook most of the feeding of first and second clutch young.

(2) That the quality of food collected, as reflected by size and type, was the same for both parents.

(3) That parents of helped broods fed less food than did parents of non-helped broods.

(4) That there was no significant difference in the quality of food (type and size) collected by regular helpers and parents.

(7) That during brooding the pattern established throughout incubation would be continued with the male spending more time on the nest than the female.

(8) That males removed significantly more faecal sacs than females.

(9) That night-time parental care energetically favoured the female.

(10) Second clutch laying: as Riflemen are double brooded it was predicted that the female's contribution towards the end of the first clutch nestling period would drop off in response to the demands of second clutch oogenesis. Conversely, during the second clutch nestling period there was not expected to be any change in the female parent's contribution towards the end of the nestling period.

Non-parental cooperative breeding

In some species non-parent birds will help care for young which belong to other birds. Brown (1978) has documented various forms of helping behaviour and outlined the theoretical implications of helper's apparently altruistic behaviour. One possible explanation given was that because helpers have been found to be related to the offspring in some cooperatively breeding species, they might improve their inclusive fitness if there was an increase in the number or survival of offspring due to their helping. It has been postulated that a special form of natural

selection, termed kin selection might explain the occurrence of helping genes in the gene pool (Brown 1978).

Soper (1975) described unusual numbers of Riflemen at nests in the Eglinton Valley, Fjordland. Cooperative breeding was observed and studied at Kowhai Bush from three points of view: what were the advantages of helping to (i) helpers, (ii) parents and (iii) offspring.

Three hypotheses relating to the benefits of non-parental cooperative breeding were considered: (a) that parents with helpers do less work than those without helpers, (b) a possible benefit to offspring was that offspring from "helper" nests were significantly heavier than offspring from "non-helper" nests and this could later influence their survival and (c) that helper behaviour benefits an individual because it improves its chances of pairing and, therefore, the kin selection theoretical prerequisite of relatedness of helpers to offspring need not apply.

B. METHODS

1.Selection of birds : The decision to use a particular pair for collecting information on parental care was based on considerations such as accessibility of the nest, stage of the nestling period and data requirements. Data were collected by watching nests from hides.

Family groups were followed during the post-fledgling period from about 15m and watched using 8x30 binoculars. The number of feeding visits by parents and helpers was scored until juveniles began to chase adults while begging for food. By this time juvenile movements prevented the gathering of reliable data. Parents which were obviously upset by observer presence were not used for data collection.

2.Data collection: Information on parental care was collected as evenly as possible throughout the daylight hours as described in the General Methods section. During the post-fledging period the birds were no longer "captive" and reliably found at will as during the nestling period and birds were followed as opportunity occurred.

The nestling period was divided into six intervals of four days each as 24 days was the average length the nestlings were in the nest. Hatching was determined by daily inspection of the nest. For the purposes of systematically gathering data on parental care the day of the first egg hatched was termed day one because Riflemen start feeding immediately after the first egg hatches.

Data from nest watches conducted in three years of study were pooled. In most cases, nests and fledglings were watched for 30 minutes. The number of food items delivered to the brood was taken to represent effort. Riflemen deliver food items to young one at a time, hence it was possible to visually size the food item relative to the bill length as was done

during courtship-feeding (section one). Estimates of food size (and type whenever possible), were used to calculate the quality of food brought to the brood.

3. Empirical information collected:

(i) The same data as recorded during the incubation period (Section two)

(ii) The number, type and size of food items fed to the brood by each feeder.

(iii) The number of faecal sacs removed by each feeder.

(iv) The number of non-feeding visits made by each feeder

(v) Which parent roosted in the nest at night.

C. RESULTS

1.Weather conditions and different birds observed during sampling:

Weather conditions were scored on each occasion parental care was watched during the nestling periods, as described in section two and the general methods. The number of observations in each summer and numbers of pairs of birds and the weather conditions observations were made in are described in Appendix 6. In summary, more than two thirds of the observations made at first clutch "non helper" nests involved at least 5 different pairs.

2.Chronology of Rifleman parental care of young

The number of nests where young were hatched and fledged during each calendar week for each year studied is shown in Appendix 3. The average length of the nestling period of 50 first and second clutches was 24.0 days (SD = 1.2, day of hatching = day 0). The time between first clutches fledging and the start of laying the second clutch averaged 8 days (SD = 4, range = 2-16 days, n = 38). Where laying was not observed directly the start was calculated using average times for incubation and laying intervals. As indicated by the size of the standard deviation the interval between fledging and laying is quite variable within and between seasons. During the 1980-81 and 1982-83 seasons the delay was longer than during the 1981-82 season.

Most breeding pairs attempted second clutches (Table 1). The pairs that produced eggs but did not hatch them, and those that did, are shown separately. Broods that hatched but were subsequently eaten by predators are included in these data because Rifleman were never known to desert nestlings and, therefore, these nests fairly represented Rifleman behaviour with respect to nesting attempts.

Table 1: Incidence of pairs with single and double broods

Year	No. pairs studied	Single brood	Double brood (eggs only)	Double brood (young only)
1980-81	12	6(50%)	0	6(50%)
1981-82	22	6(27%)	2(9%)	14(64%)
1982-83	29	18(62%)	2(7%)	9(31%)
1983-84	28	9(32%)	1(4%)	18(64%)

The number of pairs that were recorded as double brooded may be an under-estimate because some second broods may not have been found. However, most pairs built second nests near the first in nest boxes which could be systematically checked. One first clutch nest was missed, as indicated by the presence of juveniles near the second nest.

The drop in second clutches in the 1982-83 season was probably due to weather. During the end of the first clutch nestling period a northwest gale with gusts up to 80 knots and with a temperature of approximately 30°C blew for about 18 hours. The storm devasted invertebrate life, especially those insects living in the outer areas of the trees where Riflemen fed.

All eggs hatched within 48 hours and most unhatched eggs remained intact in the nest bowl.

3. Cooperative Breeding

A. Description

In this report the term "helper" refers to a non-parent Rifleman participating in parental behaviour. Cooperative breeding in Rifleman can be described using the two criteria: (1) who the helpers are and (2) by how much work they do at a given nest.

Helpers were nearly all unpaired adults or juveniles of either sex. In the case of juveniles, almost all were first clutch offspring helping at their parents' second brood. Thus, they were related to the broods.

Otherwise there was no known genetic relationship between the other helpers except in one case. The other helpers were all unpaired adults and nearly all males.

Helpers participated in all forms of parental care except brooding during the nestling and post-fledging periods. These included feeding young, removing faecal sacs from the nest, defending young and emitting alarm calls in the presence of a predator or other threat.

Apart from age, the other characteristic distinguishing helpers was the extent to which they helped. Two classes were identified and termed "casual" and "regular" helpers. Casual helpers participated in parental care irregularly by arriving at the nest only every odd hour and not necessarily consistently day after day.

Regular helpers usually started contributing consistently by about day 8 of the nestling period. Their behaviour was more predictable because, once they had started, they could be reliably seen feeding the brood consistently throughout the nestling period all day at a higher frequency than casual helpers. Also, regular helpers attended only one nest. However, sometimes there was more than one helper at a nest.

Both casual and regular helpers continued to help after fledging but only in one case did a helper of a first clutch help again at the second. Most juveniles from first clutches who helped at their parents' second clutch were only casual helpers. However, the extent to which helpers helped was not as easy to determine during the post-fledging period because of the difficulty of observing some family groups. Prior to fledging, nests were periodically watched to determine whether helpers were present.

Thus Soper's (1975) description of polygamously breeding Riflemen in the Eglinton Valley, Fjordland, is probably incorrect. There was no sign of polygamy in either study area as only two occurrences of unusual numbers of birds occurred at nests before the nestling period was well underway.

One involved two males building a nest and another involved two males attendant at an incubating nest. In neither case did the second male stay around for long.

The other potential signs of polygamy occurred during egglaying. One nest contained nine eggs - four more than the usual maximum of five. It was apparent that more than one female was laying in the nest and an unpaired female was seen regularly in the territory of the pair concerned. The breeding pair deserted the nest. The same thing happened to this pair the following season. A sixth egg was laid possibly by an unpaired female who was seen in their territory a number of times during egglaying.

Other unusual clutches involved eggs laid within the regular 48 hour interval. For example, one female laid three eggs within 63 hours whereas normally she would have taken 96 hours. It seems likely that occasionally the phenomenom of "dumping" occurs with Riflemen where a female lays an egg in another's nest. Dumping was possible since nests were left unattended during egglaying. Further, it is possible that if dumping occured prior to clutch completion the pair would not desert the nest.

Some of the potentially harmful effects of helper presence include: consumption of food needed by breeders or their young, attraction of predators to the nest, cuckoldry of the alpha male, displacement of a breeder, and killing or injuring eggs and young. Most of these effects could not be measured in this study. However, a possible attempt at cuckoldry was seen when an unpaired male from the main study area flew over the 200m of mainly open pasture from its "territory" to the near side of the pilot study area and mounted a female of another male who was feeding her fledglings. This incident was not seen by the alpha male. The copulating male was later seen back in its territory.

Despite many of the helpers being adults there was no evidence of a helper displacing a breeder or acquiring another's mate. Also there was

no evidence of helpers killing or injuring offspring as there was no significant difference in fledgling weights or numbers between helped and non-helped nests (see section 4).

B. Incidence of helpers

The figures for the incidence of the two types of helping (Table 2) are probably conservative because although all nests were watched to ascertain if helping occurred, there was still the possibility of not noticing casual helpers as they so infrequently attended nests. Further, it is possible that not all nests in the main study population were studied.

Table 2: Incidence of helpers at nests

Clutch + year	Regulars only	Casuals only	Casuals + regulars	Total nests with young*
A. Main study area				
1980-81				
First	1(17%)	2(33%)	3(50%)	6 (100%)
Second	0	3(50%)	0	6 (50%)
1981-82				
First	2(13%)	6(40%)	3(20%)	15 (73%)
Second	0	2(20%)	0	10 (20%)
1982-83				
First	1(7%)	2(14%)	0	15 (20%)
Second	2(29%)	4(58%)	0	7 (87%)
1983-84				
First	2(17%)	1(8%)	0	12 (25%)
Second	0	1(10%)	3(30%)	10 (40%)
B. Pilot study area				
1981-82				
First	0	0	0	9 (0%)
Second	0	5(83%)	0	6 (83%)
1982-83				
First	1(8%)	0	0	12 (8%)
Second	0	2(50%)	0	4 (50%)
1983-84				
First	0	0	0	14 (0%)
Second	0	2	2	7 (0%)
C. Overall incidence (both areas)				
First	7(8%)	11(13%)	6(7%)	83 (28%)
Second	2(2%)	19(38%)	5(10%)	50 (50%)

note: * percentages indicate the occurrence of both types of helping

At some nests more than one regular or casual helper occurred. The

most birds that were observed helping occurred at a second clutch nest where four first clutch offspring became regular helpers in addition to an adult female who was the mother of the maternal bird. Five other broods were found with regular helpers known to be related to the parents. Two involved the same adult male helping its parents at both their first and second clutches of the season. One helper was an adult female helping its mother's second brood of the season. In this case the helper was not known to be related to the male parent. The other two instances included a male and a female juvenile from the current season's first brood helping at their parents' second brood.

The other instances where regular helping occurred are listed as a series of case histories below. All occurred at first clutch nests and involved unpaired adult males unless otherwise stated ("NB" = non-banded birds).

C.Case histories

(i) Regular helper

Case #1(RM/gR-83/84) Unrelated and unpaired. Bred successfully the previous season in an adjacent territory. Did not pair with offspring of the brood aided.

Case #2(m/BgY-82/83) Unknown origin, unrelated and unpaired. On about the 14th day of the nestling period the paternal male died or disappeared. The helper and female parent continued to feed the brood until day 16 when the nest was vandalised. The two paired and subsequently reared a brood that season.

Case #3(NBmale130A-81/82) Unknown origin. Did not pair subsequently with a female offspring of the brood aided.

Case #4(M/YB-81/82) Unrelated but from an adjacent territory. Started helping on or before day 11 of the nestling period. Its mate disappeared early in the season 45 days prior to the male's starting day as a helper. Paired with a juvenile female of another pair in the same season.

Case #5(NBmale167-81/82) Unpaired and unknown origin but previously seen frequently about the territory. Started helping on or before the ninth day of the nestling period. This bird paired with a female juvenile from the brood which it was aiding and successfully bred two broods the next season.

Case #6(NBmale6-81/82) Unpaired and unknown origin. Started helping before the nineteenth day of the nestling period. This bird paired with a juvenile female from the brood which it helped. However, they were not seen again in subsequent seasons.

Case #7(M/RY-81/82) Unrelated and probably did not breed the previous season as it was seen helping the same pair for two seasons. Helping started prior to day 8 of the nestling period. Pairing could not be definitely ascertained but it was seen apparently paired with a juvenile female from the brood it helped. However, they were not seen again in subsequent seasons.

Case #8(M/WY-81/82) Bred successfully the previous season and had started to breed earlier in the season when it helped. A stoat had killed its mate and first clutch nestlings. Within four days it had started helping at its neighbours' nest which was no more than 13 days into the nestling period. The male subsequently paired with a juvenile from the nest where

it had helped but was not seen in following seasons.

Case #9(M/RR-80/81) Unknown origin. Started helping on or before the 6th day of the nestling period. The nest was preyed on or before the day the birds fledged so it was not possible to determine the outcome of any pairing. This male was not seen again in following breeding seasons.

Case #10(YM/-80/81) Unknown origin. Helping started on or before day 9 of the nestling period. Subsequently this bird paired with an unbanded female which could have come from the brood the male had helped because one fledgling escaped banding. They bred successfully the following season.

Case #11(WM/-80/81) The history of this bird was unknown. Helping started on or before the eighth day of the nestling period. The following season the bird was found to have paired with an unbanded female and successfully raised a brood. It was possible that this male paired with a female from the helped brood (which were all banded), lost her, and paired with another female.

Case #12(WM/RB-80/81) Nothing was known about this bird's background. It started helping on or before day 3 of the nestling period and stayed with the group without pairing. The next season it helped the same pair as a casual helper but was not seen again afterwards.

Case #13(WM/BR-80/81) This bird was the only other female to regularly help apart from those mentioned earlier helping their relations. It helped at the same nest as the male "#12" above and started on or before day 10 of the nestling period. After the nestlings fledged it was never seen again.

Case #14(NBmale-80/81) Another bird which helped at the same nest as helpers "#12" and "#13" but started on or before day 3 of the nestling period. It was not known if it paired possibly because it was unbanded.

(ii) Selected casual helper instances

The following examples of casual helping have been chosen because they involved adult banded birds and therefore something was known of their history. The examples relate to the nests at which they were seen most frequently. Although these casual helpers visited other nests their contribution there was smaller than at the nests described here. Unless otherwise stated all the individuals were unpaired adult males who helped feed young at first clutch broods.

Case #1(M/RB-80/81) After successfully rearing a first clutch brood the female disappeared. Soon after, the male started to help at the second clutch of its neighbour on the sixth day of the nestling period. This brood was partly destroyed by a predator and was deserted. The helper was seen as a casual helper the next season at the first clutch of its neighbour. It disappeared before this clutch fledged.

Case #2(M/Y-80/81)The mate of this male had disappeared the previous season after the pair had successfully reared one brood. Helping started at least by the thirteenth day of the nestling period of its neighbour's first clutch. It paired with a juvenile from the brood which it helped and successfully reared two broods the next season.

Case #3(M/WgY,YM/gR-82/83) An instance occurred where a pair failed to hatch a clutch and both helped feed the neighbouring pair's offspring. The pair stayed together and attempted to breed the following season but

again their eggs did not hatch.

Case #4(BM/R-82/83) This bird was a successful breeder in previous seasons and reared a first clutch brood in the season when it started to help. After the first clutch brood fledged its mate disappeared. About five weeks later it was seen attempting to feed the fledged offspring of its neighbour's second brood. At this stage the parents chased the helper off most of the time. About a week after the day of fledging the male parent disappeared. The helper persisted in helping with progressively less opposition from the female. After the young were independent the helping male was seen paired with the maternal bird and they successfully reared at least three broods during the following two seasons.

Case #5(BM/YBW-83/84) This was the only instance where a male left its mate despite having successfully reared a brood earlier in the season. After leaving, it helped at a neighbouring second clutch nest but was not seen to pair with a female from the brood. This bird also helped at another pair's second clutch nest with the same outcome. The bird was one year old.

Case #6(GM/BR-83/84) As far as was known this female yearling was unpaired in the season she helped. She was a yearling daughter of the male parent from the previous season.

Case #7(M/YgY,gM/YgB-83/84) This pair helped at their neighbours' second clutch nest after the helping pair deserted their first clutch. Neither bird was closely related to the parents of the clutch being helped and the helpers remained paired.

Case #8(gM/RgY-83/84) Involved an unrelated yearling bird helping at a second clutch nest. It is not known if this bird later paired.

Case #9(YM/B-81/82) The bird helped at three different nests in the one season. One of these nests was adjoining its natal territory. Apparently it was unrelated to any of the parents. However, it did not appear to acquire a mate as it was still unpaired the next season and died before the following one.

There were 62 birds which helped casually with first and second clutch broods. Of these, 30 were unpaired adults - 29 males and one female. The remaining helpers were juveniles from the current season helping with their parents' second clutch. Of these 14 were males and 18 were females.

Of the adult males which helped casually, 11 were banded and 18 were not. It is possible that some of the unbanded males were counted twice because casual helpers did help at more than one nest in one season and possibly as a casual helper in two consecutive seasons (eg casual helper case #1). Two banded birds were seen at two different nests during the same season and one banded bird was seen at three nests during the same season. Thus the figure for the number of unpaired male adult casual helpers is probably slightly exaggerated.

The one female adult which helped casually was a daughter of one of the parents it helped. The only other cases of unpaired females involved two which disappeared within a few weeks of being noticed. One was unbanded and the other was a yearling seen near its parents' territory.

Of the regular adult male helpers, 5 (26%) were males which paired with females from the brood they helped. Of the casual adult male helpers 2 (12%) involved similar pairing, one with a juvenile and one with the maternal bird.

The regular helpers that were related to the parents of the nest which they aided did not pair with the offspring from that nest. Only two cases of incest occurred. One involved a brother-sister pair from different generations. However, their nest was never discovered and it is not known if they bred. The other instance involved a father-daughter pair which fledged double broods in at least two consecutive seasons on the home territory after the original female disappeared.

D.Pairing of juveniles

In attempting to explain why unpaired birds should help it was important to consider when birds paired. As is indicated by the surplus of unpaired adult males helping, very few female Rifleman started a season without a mate. All juvenile females and most juvenile males paired in the season they were hatched with other available juveniles or adults. Apart from the birds whose partners died these pairings were permanent.

E.Parent-helper aggression

Aggression from parents was shown towards both types of helpers. Despite this there was noticeably little aggression towards regular helpers from parents. The latter often "gave way" to helpers when the birds queued around the entrance of the nest to feed young. On the other hand one of the most overtly aggressive acts seen occurred between a male parent and a male regular helper. The parent went into the nest after the helper which had entered to feed. The parent was next seen pulling the helper out of the nest by the leg along with much protestation. This occurred at about day 9 of the nestling period and no further aggression was seen. A similar pattern of reduced aggression as the nestling period progressed was seen at other regular helper nests.

F.Observations of helper behaviour towards females

Case #1 On 19/11/81 a regular helper adult male was seen with a juvenile female from the brood it had helped. As they were foraging they passed close by an unused nest box. When they were directly above it the male flew down to the perch which was built onto the box immediately in front of the entrance. Then it made slow-moving entries to and exits from the box with its wings slightly drooped. There was no apparent reaction from the female.

Case#2 The same male as above was observed reacting to the presence of a foreign adult female nearby. When the male saw her it flew up to her chattering excitedly and then repeatedly flew back and forth from her to a nearby unoccupied nest box. Upon reaching the nest box the male entered and exited slowly in a similar manner to that described above. This procedure was alternated with flying back to the female and moving about her in an excited fashion.

Case #3 A casual adult male helper approached the family which it had been helping. The young had fledged and were still being fed by their parents. The helper repeatedly approached an individual juvenile female without food and upon reaching her emitted the short punctuated call adult Riflemen give to elicit juvenile begging. After this occurred several times the agitated looking male mounted the female briefly and then was driven off by the male parent.

Case #4 In December 1981 an adult male casual helper from the main study area was seen in the pilot study area. This was an extraordinary occurrence as it was only the second instance of birds crossing from the main study area to the pilot study area. The temporary emigrant joined a

family group with recently fledged young foraging on the side nearest to the main study area. The helper appeared quite excited and was seen to mount the female parent for about 3 seconds. The helper's behaviour was the only incidence which could be construed as being an attempt at cuckoldry. As with all copulation behaviour witnessed it was not possible to tell whether cloacal contact had occurred.

4. Sex ratio of adults

In making an estimate of sex ratio the incidence of helping and the numbers of banded birds were taken into account and the assumption was made that all breeding pairs used nest boxes. The latter assumption was valid in the pilot study area at least because all but one breeding pairs used boxes and nearly all birds were banded.

In the main study area some pairs did not breed in nest boxes and they and their offspring went unbanded. However, the proportion of birds that were nonbanded in consecutive seasons were : 1980-81 16%, 1981-82 15%, 1982-83 5%. These figures probably over-estimate because most non-banded birds were males which were seen casually helping at nests. Banded casual helpers visited on average two different nests each year they were studied. This figure has been used below to halve the number of adult nonbanded casual male helpers (Table 3). Thus the column headed "casual male" includes the number of banded birds plus the corrected figure for nonbanded birds.

Table 3 Numbers of Rifleman at the start of each season

	Breeders		Helpers		
	M	F	Casual M	Regular M	Regular F
1980-81 Main	14	14	3	5	1
1981-82 Main	22	22	11	4	0
Pilot	13	13	0	0	0
1982-83 Main	18	18	2	0	1
Pilot	18	18	0	1	0

M = males, F = females

The adult sex ratios reflected a marked surplus of males in the main study area in two seasons, otherwise the sex ratios were close to unity (Table 4).

Table 4 Adult sex ratio at the start of each season

Season	1980-81	1981-82		1982-83		1983-84
Study area	Main	Main	Pilot	Main	Pilot	Pilot
Males	22	37	13	20	19	20
Females	15	22	13	19	18	21

In both study areas there appeared to be more males than females at the start of each season. This is supported by the fact that most of the nonbanded birds at the start of each season were males (Table 5).

Table 5 Sex of nonbanded birds at the start of each season

Season	1981-82		1982-83		1983-84
Study area	Main	Pilot	Main	Pilot	Pilot
Males	6	1	7	3	2
Females	0	1	0	2	1

5. Division of Labour

A. Brooding

(i) Attentiveness

Attentiveness while brooding was measured by dividing the time spent in the nest by the time the nest was observed. Brooding decreased as the nestling period progressed and males spent more time brooding than females (Table 6). However, there was no significant difference in the length of

the sitting spells males and females spent brooding except in two cases. They occurred during days 1-4 in the second and third periods during the day (Wilcoxon matched pairs sign rank test, $T = 68.0$, $P < 0.05$; $T = 63.5$, $P < 0.05$).

Table 6 Attentiveness during brooding (mean, SD)

	Days 1-4	Days 5-8	Days 9-12
A. First clutch:			
Male	0.39, 0.19	0.14, 0.18	0.01, 0.05
Female	0.28, 0.18	0.12, 0.12	0.01, 0.04
Combined	0.68, 0.21	0.26, 0.25	0.03, 0.09
N watches	63	37	48
B. Second clutch:			
Male	0.32, 0.18	0.23, 0.18	0.09, 0.14
Female	0.28, 0.17	0.17, 0.15	0.06, 0.11
Combined	0.59, 0.25	0.39, 0.31	0.14, 0.20
N	68	55	45

(ii) Diurnality of brooding behaviour

Data for males and females were combined for the first eight days of the nestling period. There was no significant difference in attentiveness between the three periods during the day although there was some indication that more time was spent brooding in the early part of the day when ambient temperatures were probably lower (Table 7).

Table 7 Diurnality of brooding behaviour over the first eight days of the nestling period

	First clutch			Second clutch		
Interval of day	Mean	SD	N	Mean	S	N
1	0.62	0.34	27	0.59	0.26	34
2	0.50	0.30	40	0.45	0.30	40
3	0.47	0.27	33	0.47	0.27	33

(iii) Sitting spells

The number of parental visits to the nest which involved brooding have been summed for each interval of the nestling period as there was no significant variation through the day. Helpers were never seen to brood.

As was expected from the results of actual time spent on the nest the number of brooding visits made by each parent was not significantly different (Table 8).

Table 8 Frequency of visits involving brooding

Days	Male parent	Female parent	Chi square	P
A. First clutch non-helper				
1-4	101	93	0.253	>0.60
5-8	19	25	0.572	>0.40
B. First clutch helper				
5-8	7	10	0.235	>0.60
C. Second clutch non-helper				
1-4	68	58	0.643	>0.40
5-8	18	14	0.805	>0.30
D. Second clutch helper				
5-8	6	7	0.000	-

B. Feeding young

(i) Food size at first clutch nests

The average size of food items which could be visually assessed were similar throughout non-helper and helper nests (Table 9).

Table 9 Average food size delivered to first clutch nests

A. First clutch non-helper						
Parent:Days	1-4	5-8	9-12	13-16	17-20	21-24
male (X)	3.7	3.8	4.6	4.2	4.1	3.9
SD	1.4	1.4	1.3	1.4	1.5	1.6
N	164	174	180	217	204	151
female (X)	3.5	3.4	4.5	4.1	3.9	3.8
SD	1.2	1.4	1.5	1.6	1.6	1.7
N	104	145	170	153	161	102
B. First clutch helper						
male (X)	-	2.7	3.1	3.4	3.4	3.3
SD		1.4	1.4	1.5	1.6	1.5
N		26	118	85	101	95
female (X)	-	2.6	3.1	3.3	3.2	3.7
SD		1.2	1.2	1.6	1.4	1.4
N		44	106	77	65	70
helper (X)	-	3.1	2.8	3.2	2.9	3.0
SD		1.0	1.2	1.3	1.3	1.3
N		11	74	63	62	145

Food sizes for parents were compared for both nest categories using the Mann Whitney U Test. There was no significant difference in the size of food items parents delivered to the nest ($P>0.05$) for each of the four-day intervals. Also there was no significant difference in the size of food items delivered between each four-day interval for any feeder. At helper nests there was no significant difference in the size of food items delivered by parents and helpers except in days 21-24 in which the female parent delivered significantly larger food items than the helpers ($U=6290.5$, $P<0.01$, one tailed test).

As indicated by the averages in Table 9, food items delivered to non-helper nests by parents were in the main significantly larger than those fed by parents or helpers at helper nests (U tests, $P < 0.05$). The single exception occurred between female parents of non-helper nests and helpers during the last four days of the nestling period (U Test, $U = 3727.5$, $P > 0.05$).

(ii) Food size at second clutch nests

As with parents feeding first clutch nests, those feeding second clutches delivered similar sized food items (Table 10) except in the first interval when the males fed significantly larger items (Mann Whitney U test $U = 6769$, $P < 0.01$). Contrary to the findings for first clutches there was no significant difference between non-helper and helper nests in the size of food items delivered to the nest by feeders, although in two instances (the parents at helper nests during days 21-24) the sample sizes were too small to warrant a comparison.

Table 10 Average food size delivered to second clutch nests

A. Second clutch non-helper						
Parent:Days	1-4	5-8	9-12	13-16	17-20	21-24
male (X)	3.4	3.6	3.8	3.9	3.9	3.8
SD	1.2	1.2	1.3	1.4	1.3	1.4
N	121	137	166	264	248	78
female (X)	2.9	3.5	3.6	3.8	3.7	3.7
SD	1.1	1.2	1.2	1.3	1.5	1.4
N	91	106	119	170	168	67
B. Second clutch helper						
male (X)	-	4.0	4.0	4.0	3.7	3.7
SD		1.2	1.0	1.4	1.1	0.71
N		36	52	51	29	8
female (X)	-	3.5	3.8	3.8	3.6	3.4
SD		0.9	1.1	1.2	1.1	1.1
N		16	15	13	15	7
helper (X)	-	3.6	3.7	3.7	3.9	4.1
SD		1.1	0.9	1.2	1.1	1.3
N		32	49	44	26	25

(iii) Types of food delivered to nests

Most of the food seen carried to the nests under observation could not be identified into the categories of "moths", Orthopterans etc. The proportion of the total food delivered that could be categorised for parents was similar - about 20% and 38% for first and second clutches repectively (Table 11).

Table 11 Proportion of identified food in each category and total categorised food

A. First clutch

Parent/ helper	% of food categorised	Food categories - % of categorised food 1	2	3	4	5	6
male	17	66	20	2	2	1	9
female	23	64	20	2	2	1	10
helpers	20	50	37	5	4	0	3
B. Second clutch							
male	38	50	17	9	2	1	20
female	38	52	13	6	6	5	18
helpers	21	68	19	3	3	1	6

key : 1 = moths, 2 = catapillars, 3 = Diptera (adults),
4 = wetas, 5 = Coleoptera, 6 = Arachnida
note : "wetas" include Hemedeina femorata , Hemeandrus and Isoplectron spp. (Or. Orthoptera)

(iv) Feeding rate at first clutch non-helper nests

Because there was no significant difference in the size of food items fed by parents at either clutch or nest category and the types of food fed were similar, frequency of food items fed per hour was used to compare parental effort in this and the following sections.

If no significant diurnality occurred, then data for the whole day can be considered for each feeder collectively for a given interval of the nestling period (Table 12).

Table 12 Average feeding rate for each period of the day

Parent	Period of day		
	1	2	3
male	13.1(11.3-14.9)	12.9(11.5-14.3)	13.3(11.8-14.7)
female	9.5(8.1-10.8)	8.4(7.2-9.6)	8.9(7.7-10.0)
N	85	111	96

Notes :-95% confidence intervals are shown in brackets
:-data pooled for the whole nestling period

The male fed on average significantly more items per hour throughout the nestling period than the female (Figure 3-1, Table 13). There were only three significant changes in feeding rate between consecutive four-day intervals for parents separately or collectively, and two of these involved parallel changes between males and females.

Table 13 Wilcoxon Sign Rank Tests between parental feeding rates at first clutch non-helper nests

Ho : that the feeding rates were the same
Hi : the male feeding rates were higher than female's

	Stage of the nestling period					
	1-4	5-8	9-12	13-16	17-20	21-24
Z	-4.00	-3.79	-2.84	-5.02	-4.18	-3.33
P<	0.001	0.001	0.001	0.002	0.001	0.001

Male parents fed between 57% to 62% of the total number of food items - about half as much again as did the females (Figure 3-2).

(v) Feeding rate at first clutch helper nests

There was no significant variation during the day in the frequency of food items delivered by any of the feeders (Table 14).

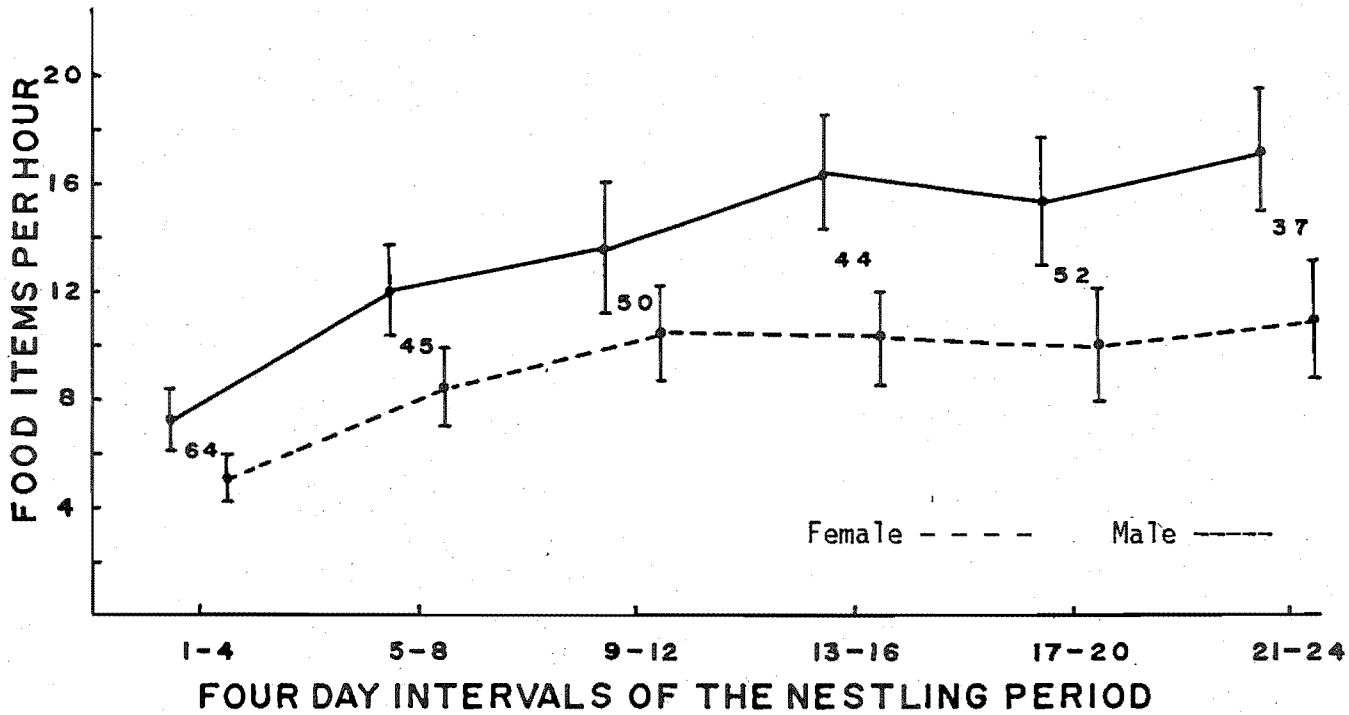


Figure 3-1 Average parental feeding rate at first clutch non-helper nests (95% confidence intervals, sample sizes indicated).

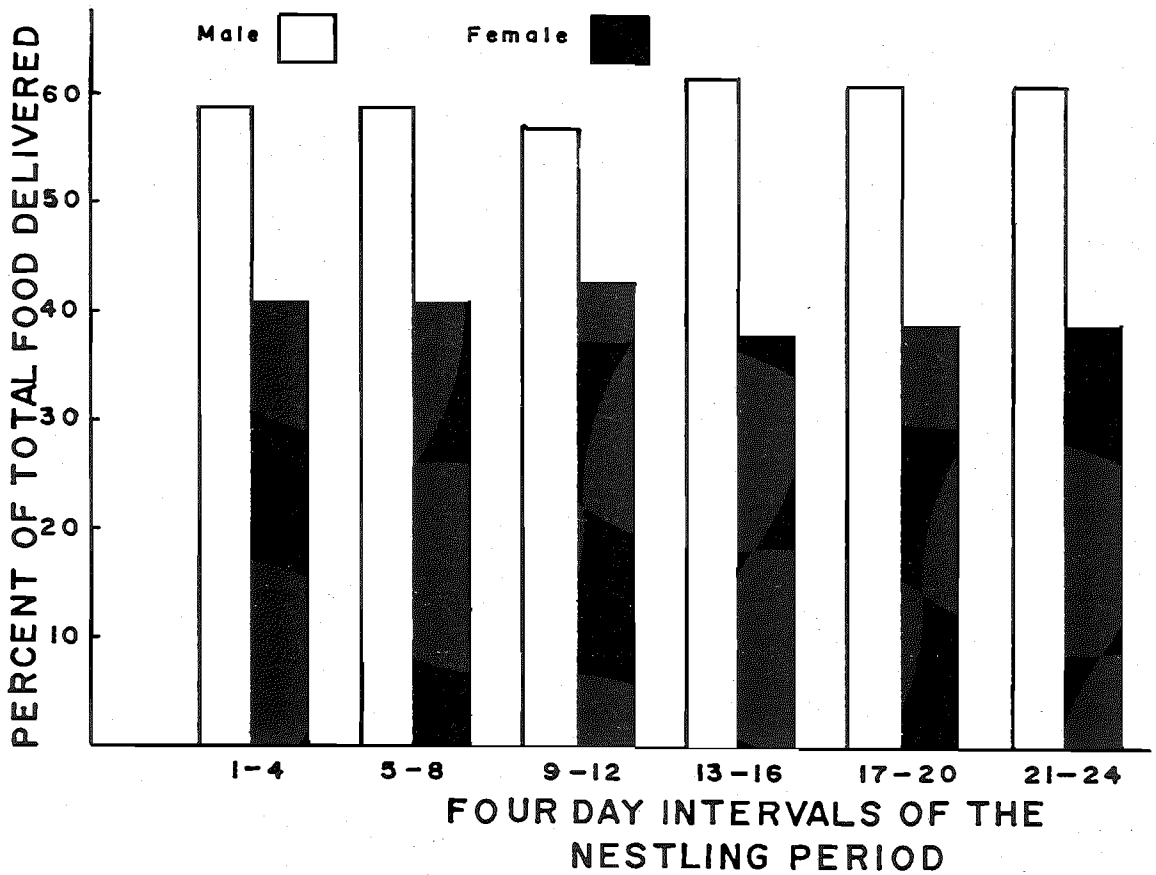


Figure 3-2 Proportion of total food delivered by each parent at first clutch non-helper nests.

Table 14 Average feeding rate at each day period for feeders at first clutch helper nests

Parent	Day period		
	1	2	3
male	12.3(10.1-14.4)	10.2(8.9-11.6)	11.5(9.8-13.2)
female	8.3(7.0-9.5)	7.6(6.4-8.9)	7.0(5.8-8.2)
helper	7.4(5.6-9.2)	7.2(5.6-8.8)	9.2(7.4-11.1)
N	57	68	60

note : 95% confidence intervals in brackets

As there was no obvious diurnality the data for each day interval of the nestling period were considered collectively. Because helping was at such a low level during the first eight days the following results describe feeding behaviour over the last four-day intervals of the nestling period.

The parents did not significantly change the rate of their feeding throughout the last four day-intervals of the nestling period (Kruskal-Wallis ANOVA H = 3.79, H = 5.53, $P > 0.05$ for males and females respectively). There were significant changes in the rate of helper feeding (Kruskal-Wallis H = 18.58, $P < 0.05$). However, none of these included significant changes between consecutive day intervals.

Considering collectively all feeder's data for each four-day interval over the whole of the nestling period there was no significant difference in the combined feeding rates (Kruskal-Wallis H = 10.41, $P > 0.05$).

A comparison of the averages of feeding rate for each four-day interval showed a similar pattern of parental care as for non-helper nests except in the second day interval (Figure 3-3). In this case the average feeding rate of the female was more than for the male. This exception might be partly explained by the small sample size for this day interval (n = 14).

The comparison between the parents indicates a changed situation as compared with non-helper nests. During days 4-8 and 9-12 there was no significant difference between the male's and female's feeding rates (Wilcoxon matched pairs test in Table 15).

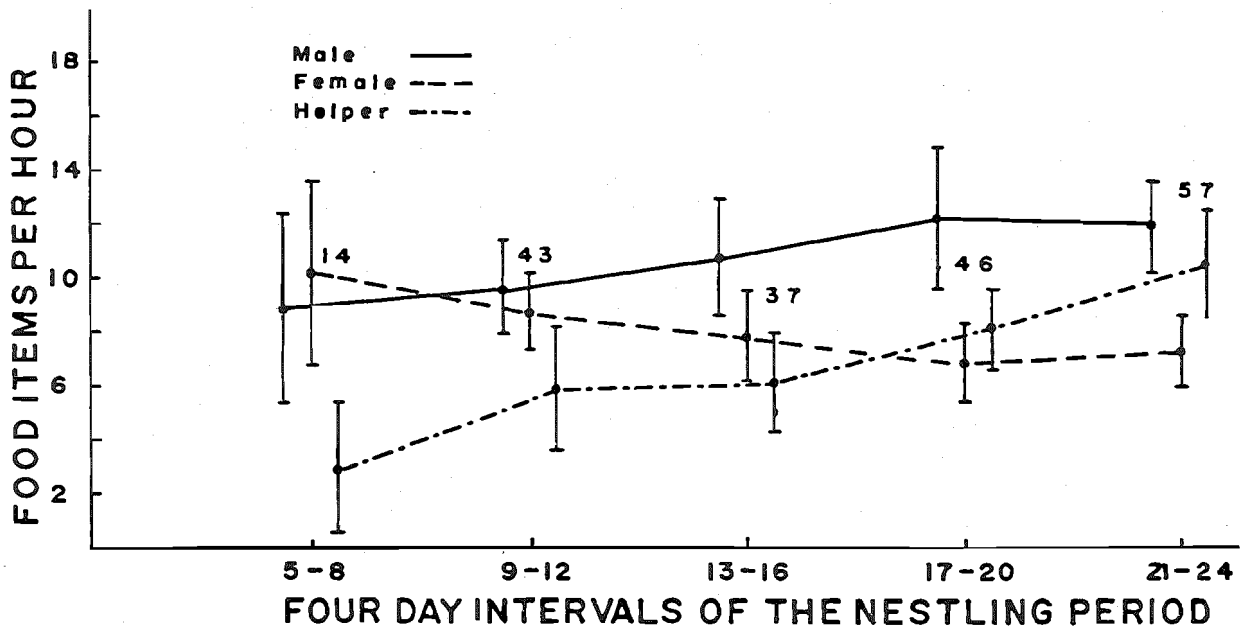


Figure 3-3 Average feeding rates of parents and helpers at first clutch helper nests (95% confidence intervals, samples sizes indicated).

However, over the rest of the nestling period the former pattern reappeared with the male feeding at a significantly higher rate than the females.

Table 15 Wilcoxon Sign Rank test between feeder's rates of food delivery at first clutch helper nests

A.Parents (Ho:male = female, Hi:male > female)

	Stage of nestling period (days)				
	4-8	9-12	13-16	17-20	21-24
Z	+0.59	-0.96	-3.16	-4.13	-4.67
P	>0.28(NS)	>0.17(NS)	<0.001	<0.001	<0.001

B.Male parent vs helper (Ho:male = helper, Hi:male > helper)

Z	-2.79	-3.21	-3.69	-2.83	-1.19
P	<0.003	<0.001	<0.001	<0.002	0.12(NS)

C.Female parent vs helper (Ho:female = helper, Hi:female > helper)

Z	-2.79	-2.39	-2.28	-1.25	+3.23*
P	<0.003	<0.008	<0.011	>0.11(NS)	<0.001

* - the significant positive value of Z indicates that the helper fed at a significantly faster rate than the female parent

The comparison of the male parent's feeding rates with the helper's indicated that the male fed significantly more than the helper except in the last four-day interval when the helpers fed almost as much on average as the male parents (Figure 3-3).

The female parent's feeding behaviour as compared with the helper's was more complicated. During days 4-8, 9-12, and 13-16 the female fed at a significantly higher rate than the helper. During days 17-20 there was no significant difference between the two and by days 21-24 the helper was feeding at a significantly higher rate than the female parent. This situation in which the helper's performance overtook the female's was due mainly to the helper markedly increasing its effort after days 4-8 and to a lesser extent because the female's effort declined slightly from this time onwards.

As with the non-helper nests the male parents contributed the greater share of food fed per hour except in days 5-8 (Figure 3-4).

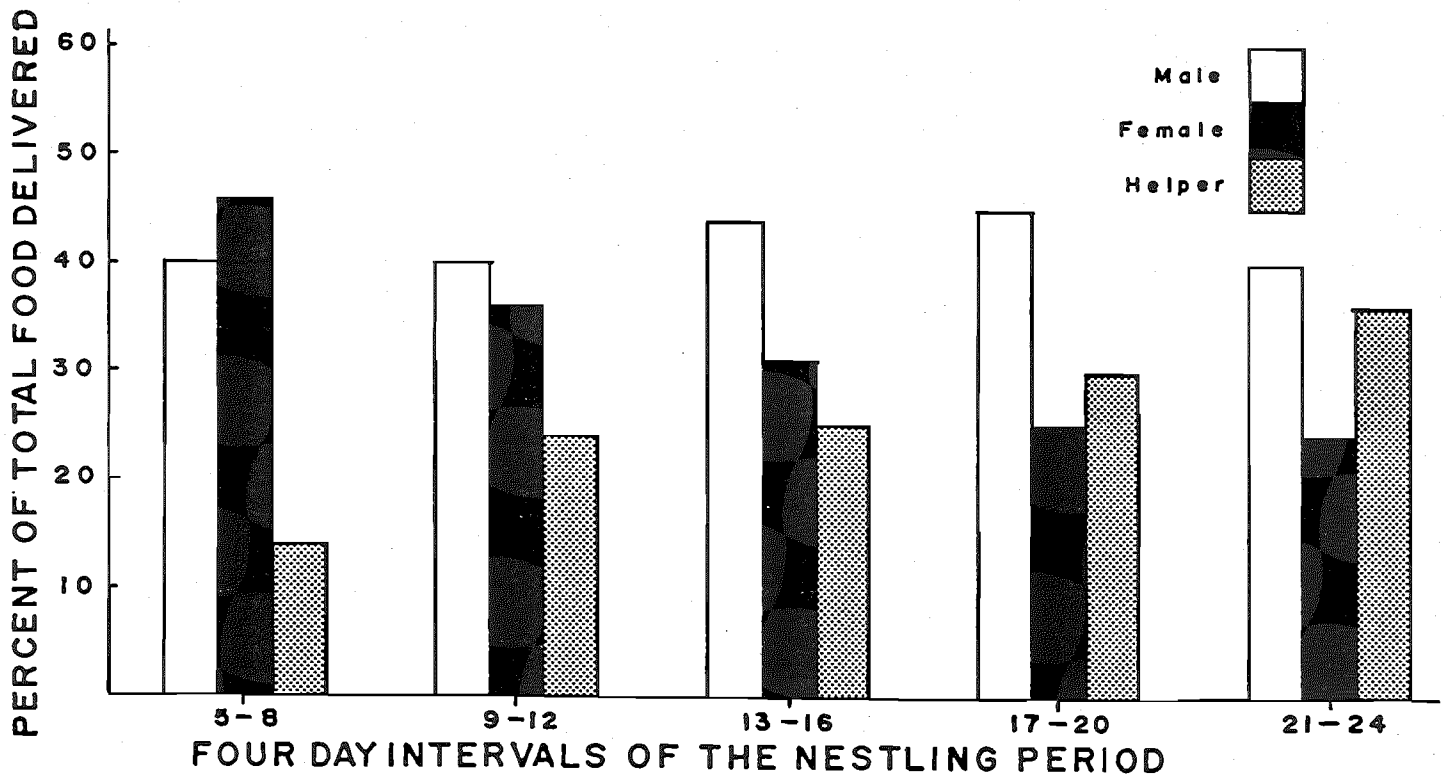


Figure 3-4 Proportion of total food delivered by each feeder at first clutch helper nests.

Their proportion remained consistent between 40-45% for the male whereas the female's relative contribution declined from 46-24%. There was a corresponding increase in the helper contribution from 14-36%. These trends reflected actual changes in the average number of food items fed per hour but the helper feeding rate showed the greatest change from 3 items per hour to over 10 items per hour.

(vi) Comparisons between first clutch helper and non helper nests

Out of the five comparable four-day intervals there were three intervals when the total food delivered per hour was higher at helper nests, one when the averages were about equal and one when the average at non-helper nests was higher (Figure 3-5). However, none of these differences were significant (Table 16).

Table 16 Comparison of total feeding rates at non-helper and helper nests

Day-interval	5-8	9-12	13-16	17-20	21-24
Mann Whitney U test stat	327	1130	902	1318	1062
P	>0.05	>0.05	>0.05	>0.05	>0.05

Although there were no significant differences between non-helper and helper nests in the frequency of food deliveries the average sizes of food items fed by both parents were significantly larger at non-helper nests except for females in the last four-day interval (U test, Table 17). Whether these differences are significant enough for the conclusion to be drawn that more food (by volume) was being fed at non-helper nests, however, remains in question. This is because actual food volume is not simply the product of the frequency and food size data.

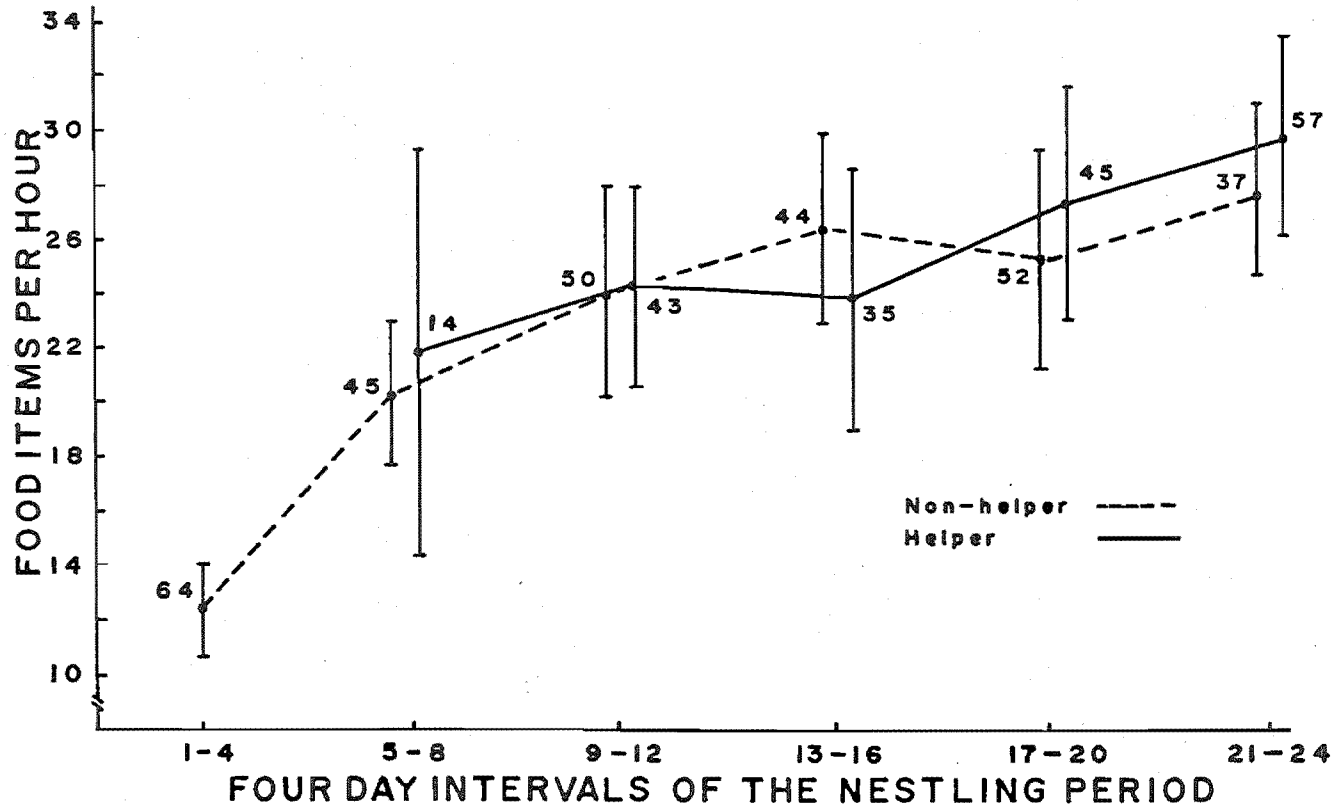


Figure 3-5 Average feeding rates at first clutch non-helper and helper nests (95% confidence intervals, sample sizes indicated).

Table 17 Comparison of food item size fed by parents at non-helper and helper nests (Mann Whitney U test)

Four day int.	5-8	9-12	13-16	17-20	21-24
Males (U)	3234	16350	11924	12722	8663
P	<0.01	<0.01	<0.01	<0.01	<0.01
Females (U)	4262	13586	7618	6378	3727
P	<0.01	<0.01	<0.01	<0.01	>0.05(NS)

Whereas male parents at helper nests fed significantly less frequently than males at non-helper nests during the last 20 days, female parents from helper nests fed significantly less in only the last 12 days of the nestling period (Figures 3-6 and 3-7, Table 18).

Table 18 Comparisons of feeding rates of parents of helper and non-helper nests (1 tailed Mann Whitney U tests: Ho:non helper = helper, Hi:non helper > helper)

Day interval	5-8	9-12	13-16	17-20	21-24
Males (U)	423	1405	1212	1491	1523
P	<0.05	<0.01	<0.01	<0.05	<0.01
Females (U)	373	1233	1023	1450	1385
P	>0.05(NS)	>0.05(NS)	>0.05(NS)	>0.05(NS)	<0.01

Both parents at helper nests benefitted from the presence of a helper because they reduced the rate at which they brought food to the nest as compared with parents at non-helper nests. There was apparently no benefit to the offspring in terms of increased food supply as there was no statistically significant difference in the rates of feeding at non-helper and helper nests (Table 16). However, the size of food items fed to non-helper nests might have meant the volume fed was higher than at helper nests. There was no obvious explanation for this difference in food size.

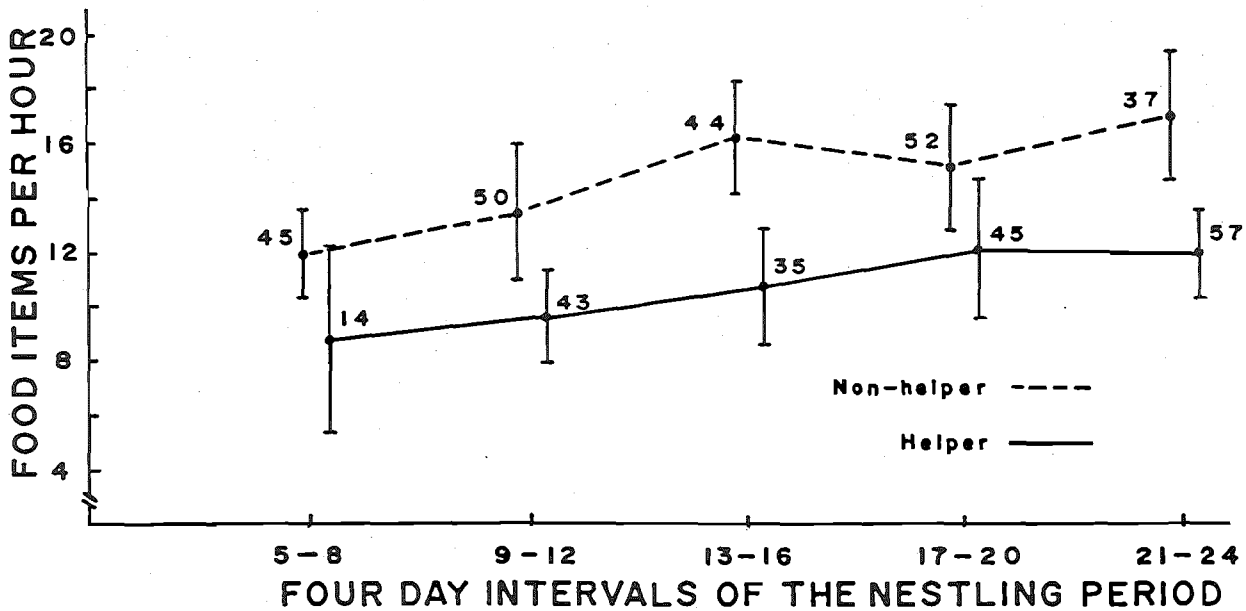


Figure 3-6 Average feeding rates of male parents at non-helper and helper first clutch nests (95% confidence intervals, sample sizes indicated).

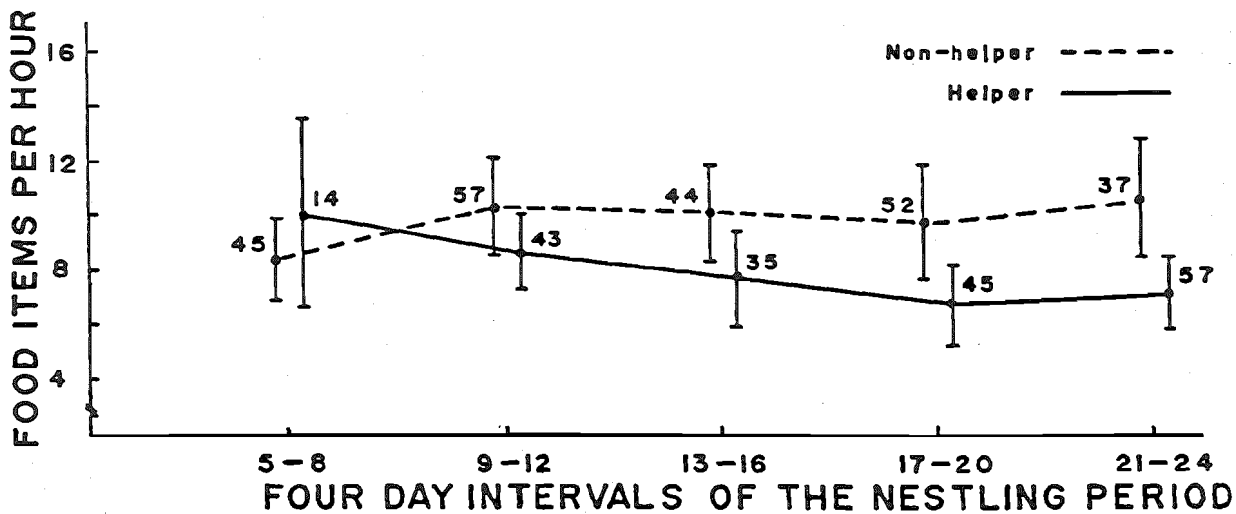


Figure 3-7 Average feeding rates of female parents at non-helper and helper first clutch nests (95% confidence intervals, sample sizes indicated).

(vii) Feeding frequency at second clutch non-helper nests

There was no diurnality in feeding behaviour for either parent at second clutch nests when data from three periods of the day were compared (Table 19).

Table 19 Average frequencies of food items fed per hour for each period of the day at second clutch nests (mean, 95% confidence intervals)

Period of the day	1	2	3
Male parent	13.3	12.5	14.5
	11.8–14.8	11.0–14.1	12.7–16.3
Female parent	8.6	8.2	8.6
	7.4–9.8	7.2–9.2	7.3–10.0

As there was no significant diurnality in feeding rates, data were pooled for each four-day interval of the nestling period. There were some significant changes in feeding rates between consecutive four-day intervals (Kruskall-Wallis ANOVA, $H = 69.88$, $P < 0.05$; $H = 44.42$, $P < 0.05$ and $H = 84.84$, $P < 0.05$ for male, female and combined feeding rates respectively).

Male parents significantly increased their rates of feeding between days 1–4 and 5–8 and between 5–8 and 9–12 (Mann Whitney U tests; $U = 2167$, $P < 0.01$; $U = 2053$, $P < 0.01$). Female parents significantly increased their feeding rate between days 13–16 and 17–20 (one tailed U test $U = 2446$, $P < 0.05$). Otherwise there were no other significant changes between consecutive four-day intervals for each parent. The combined feeding rate significantly changed in similar manner to the male parent's with significant differences between days 1–4 and 5–8, and between 5–8 and 9–12 (one tailed U tests, $U = 2204$, $P < 0.01$; $U = 1977$, $P < 0.01$).

The male parent's rate of feeding was significantly higher than the female's (Table 20, Figure 3-8).

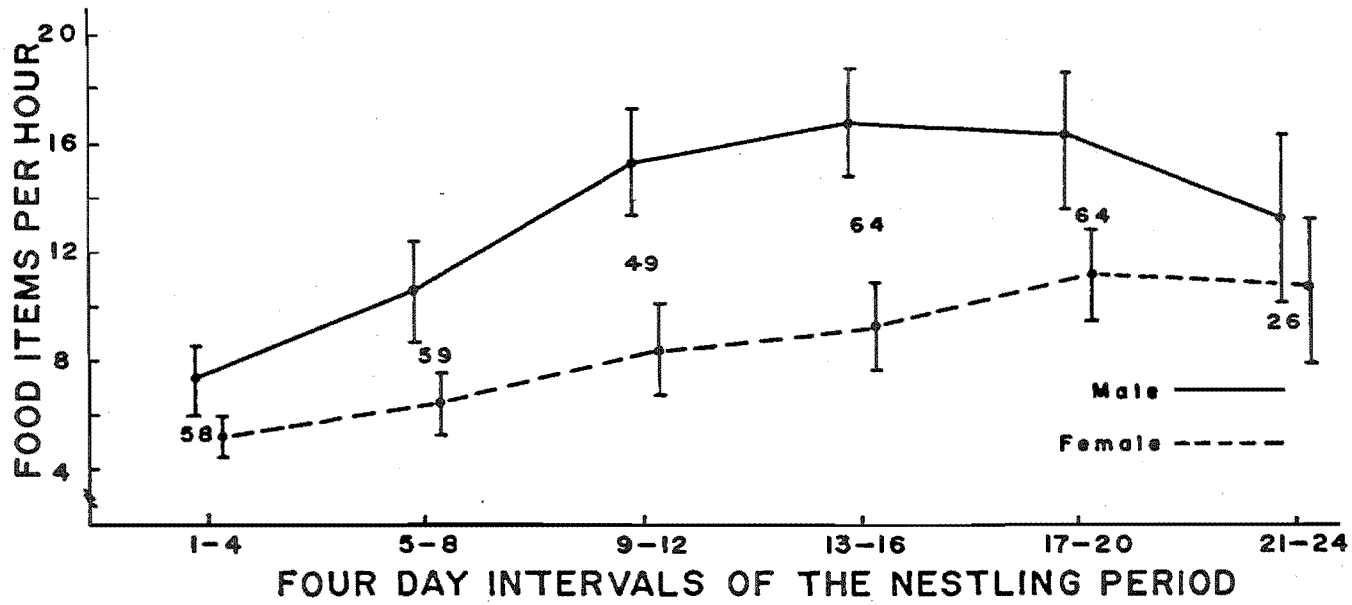


Figure 3-8 Average feeding rates of parents at second clutch non-helper nests (95% confidence intervals, sample sizes indicated).

Table 20 Wilcoxon sign rank test on paired parental feeding rate data for each day interval at second clutch non-helper nests

Four day int.	1-4	5-8	9-12	13-16	17-20	21-24
Std normal deviate (Z)	-3.39	-4.13	-4.55	-4.98	-3.95	-1.46
P	<0.001	<0.001	<0.001	<0.001	<0.001	0.072(NS)

Male parents contributed from 55-65% and females from 35-45% of the total food (Figure 3-9). Thus the relative contributions were comparable with those at first clutch non-helper nests.

(viii) Second clutch helper nests

Two regular helper nests were intensively studied. Thus there were too few data to test for diurnality, to compare feeding rates between consecutive day-intervals or with parents from non helper nests. The feeding rate averages are shown in Figure 3-10. In order to compare statistically the contributions made by each feeder the data for the whole nestling period were treated collectively. Male parents and helpers fed at a significantly higher rate than female parents (Table 21). Thus despite the few data there appears to be an important contribution from regular helpers at second clutch helper nests.

Table 21 Wilcoxon sign rank test on paired feeding rate (FR) data for all feeders from all day intervals combined for second clutch helper nests

A. Ho:male parent FR =female parent FR, Hi:male FR >female FR
Z = -4.39, P < 0.001, significant - accept Hi

B. Ho:female parent FR = helper FR, Hi:helper FR > female FR
Z = -3.90, P < 0.001, significant - accept Hi

C. Ho:male parent FR = helper FR, Hi:male FR > helper FR
Z = -0.24, P > 0.05, not significant - accept Ho

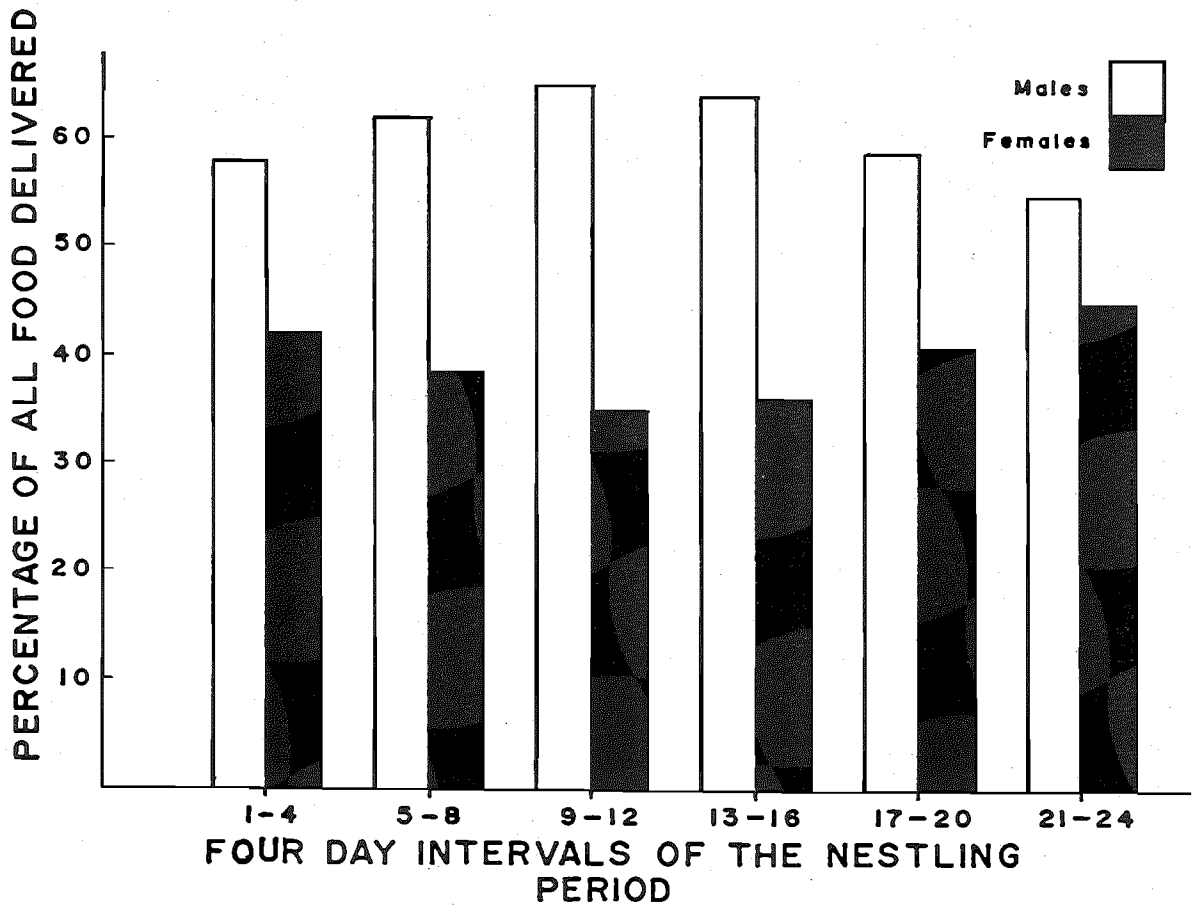


Figure 3-9 Proportion of food items delivered by parents at second clutch non-helper nests.

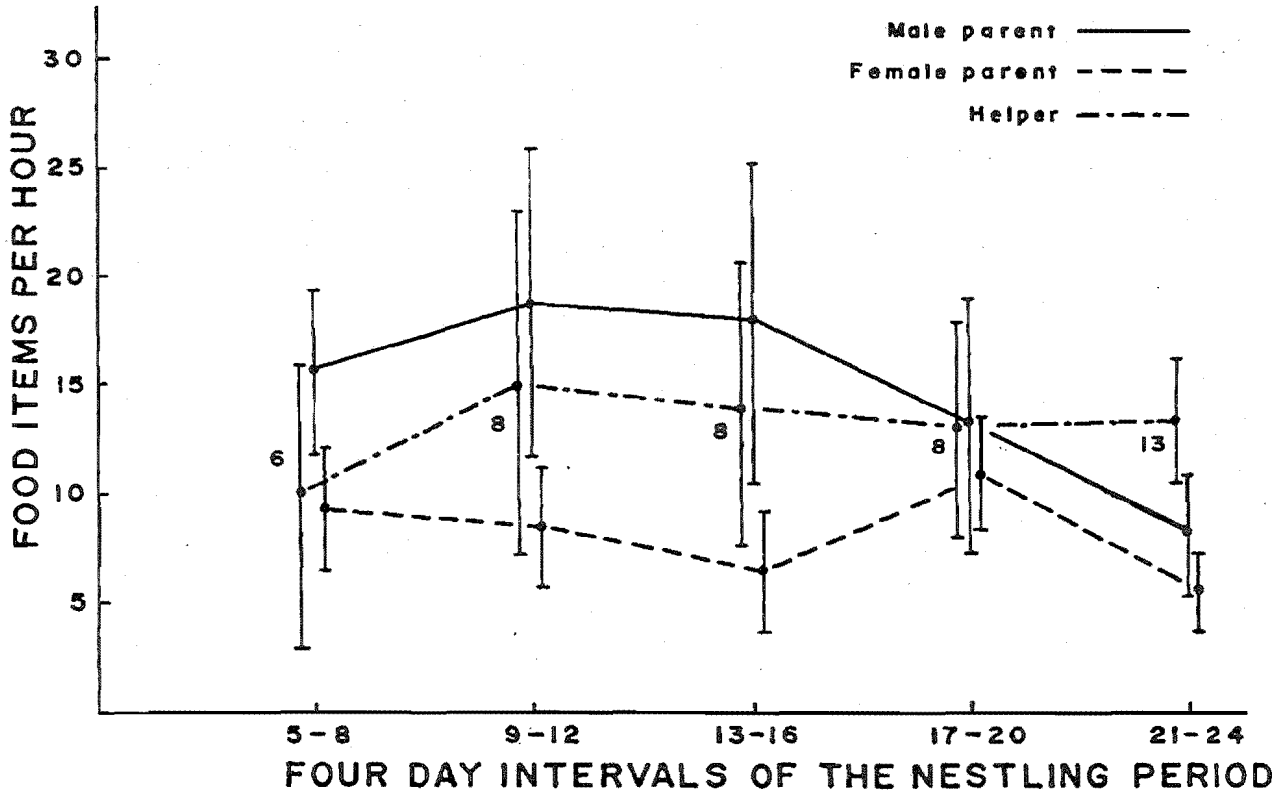


Figure 3-10 Average parental and helper feeding rates at second clutch helper nests (95% confidence intervals, samples sizes indicated).

No statistical tests of differences in the combined feeding rates for all feeders at non-helper and helper nests are warranted because of the small sample sizes in the helper category. However, the helper nests appeared to follow the same pattern as the non-helper nests with an increase in feeding rate in the early stages and some decline towards the end of the nestling period (Figure 3-11).

C. Other forms of parental care during the nestling period

Apart from visits to the nest to feed young five other categories of parental care were recorded. One involved a parent entering the nest without food and exiting almost immediately. Two others involved a parent visiting the nest - one to inspect the nest; one just to alight on the perch and fly off. These two will be considered together. Another involved the parent entering the nest and removing a faecal sac.

There was no clear trend that reflected the pattern of behaviour of feeders delivering food. The two variables which conceivably involved the greatest outlay of energy (visits into the nest and faecal sac removals) were equally shared in the latter case, and in the former made significantly more often by the male except at first clutch helper nests (Table 22).

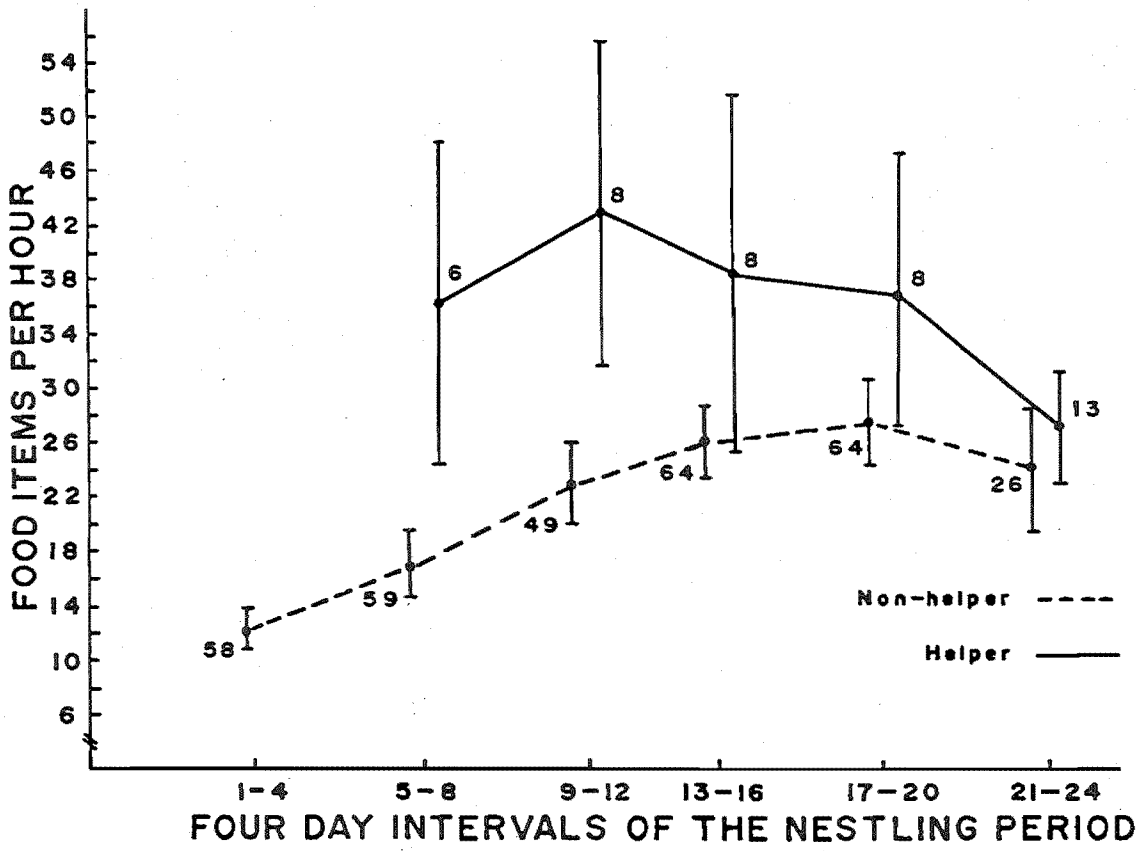


Figure 3-11 Average combined feeding rates at second clutch helper and non-helper nests (95% confidence intervals, sample sizes indicated).

Table 22 Chi square tests on nest visits comparing parents' total number of visits

- table shows significant comparisons and hypothesis accepted
Parents: Ho: male = female, Hi: male > female

	1st clutch non helper	1st clutch helper	2nd clutch non helper	2nd clutch helper
Visits into the nest	S, Hi	NS, Ho	S, Hi	S, Hi
Removal of faecal sacs	NS, Ho	NS, Ho	S, Hi	NS, Ho
Visits to entrance	NS, Ho	S, fem>male	NS, Ho	too few data

Chi square tests comparing parents and helpers showed that parents made significantly more visits than helpers ($P<0.05$) except in the following cases : (i) at first clutch helper nests helpers made significantly more visits to the entrance than female parents; (ii) at second clutch helper nests helpers made significantly more visits into the nest than female parents.

The other minor measures of parental effort were the frequencies of visits delivering and taking out feathers by feeders. The numbers of visits of each type were trivial against the other variables mentioned but for the non helper nests the male parents made about two times more visits than the females. As these visits occurred mostly in the first eight days before helping started a comparison with helpers is not warranted.

D. Night time parental care

Nests were checked at night by inserting an anuscope through the nest entrance. Usually one could see around the nest bowl and determine if one or two adults were in the nest. On each of the 27 occasions when first clutch nests were inspected during the nestling period, only the female was present in the nest. The inspections were made between 8 nests in October 1983 on about the same number of occasions. Two other nests were

inspected once. The observations were all made within the first half of the nestling period between 1930 and 2200 hours. Hence observations started about an hour after sunset. On eight of the occasions the female had placed feathers partially blocking off the entrance of the nest.

E. Post fledging care of young

(i) Natural history

Nestling Riflemen were seen fledging three times. The adults continued to feed the young in and out of the nest until all had left. Fledging was completed within two hours with young reluctant to fly and preferring to remain in a group perched high up even if approached. When they did move it was with short flying hops. Fledglings had conspicuous plumage with dark spots or stripes underneath concentrated towards the chin. The crown feathers had dark striped plumage which later reverted to the adult plumage of dull grey in males and brown-black stripes in females. Elsewhere the plumage resembled that of the adults. Thus the sexes could be readily distinguished.

Fledglings from first and second clutches reached independence within four to five weeks after leaving the nest. Because the average time between fledging the first clutch and laying the second was 9.3 days (SD = 5.7, n = 27) and laying the average second clutch took 5-7 days, there were about three weeks during which parents had to cope with feeding dependent fledglings and laying or incubating the second clutch.

Observations of parental effort feeding fledglings were made on 31 different first clutch broods and 11 second clutch broods. There was apparently no difference in the time it took fledglings from first and second clutches to gain independence so the description of acquiring independence below applies to birds from both clutches.

During the first week fledglings rarely took any food themselves. Their movements were few and most time was spent perched in groups while the parents flew to them delivering food. They gave a continuous single note piping call and begged using another longer call. Begging also included gaping and displaying the dull orange-yellow of the buccal cavity. In Riflemen the rictal flange was similarly coloured but not conspicuous.

By the tenth day the fledglings had started to display concerted foraging behaviour. However, their foraging was not very successful and nearly all their food was received from the adults. Begging behaviour included chasing adults and calling constantly. After the second week the young were dividing their time about equally between foraging for themselves and chase-begging. However, most of their food was apparently received from the parents.

Over the third week after leaving the nest the fledgling's self-feeding became much more evident although adult feeding was still frequent. Feeders sometimes left young for periods during which young successfully fed themselves. Often the groups split up as individuals or into pairs which chase-begged feeders. By the end of 21 days juveniles were taking most of their own food, although some juveniles seemed more competent than others.

After three weeks the fledglings were only occasionally seen together and chase-begging occurred infrequently. Feeding by adults still occurred, although by the end of the fourth or fifth week any form of parental care was rare.

Parents and helpers did not feed particular individuals as did Robins (Flack, 1979). The smaller amount of food female parents fed was also reflected in the manner they behaved with fledged family groups. Females often foraged alone but within sight of their family group, apparently just far enough removed to avoid begging.

(ii) Sibling aggression

Sibling aggression was frequently observed among fledgling groups. The greater number of cases involved female fledglings in overtly aggressive acts towards males. Three examples are listed below:
Case #1: 15/11/82 (first clutch). Fledglings had been perched in a bunch for about 15 minutes. One of the female fledglings chased a male and pecked it continuously. This occurred five days after fledging.
Case #2: 4/11/83 (first clutch). A female fledgling was seen pecking and jostling a male fledgling for a favoured perch and displaced the male. This happened seven days after fledging.
Case #3: 21/11/80 (first clutch). Group of three juveniles - two males and one female perched as a group awaiting feeding. The female continuously pecked a particular male until it was forced off the perch.

Aggression between juvenile siblings also occurred between young from different clutches. Older juveniles from first clutches were occasionally seen chasing and pecking second clutch fledglings. It was possible that this was due to birds trying to obtain food as occasionally the parents would feed a first clutch juvenile even with second clutch ones around.

(iii) Juvenile pairing

Juveniles paired after independence from late December into March. Pairing occurred between juveniles hatched in the same year or with adults. All combinations of pairing occurred at the first opportunity. Only two "divorces" were known. One of these involved a bird emigrating. The same types of pairing occurred in populations other than the two study populations such as in the Hapuka River Catchment near Kaikoura (NZMS 1 S46). Thus unpaired adults at the start of a breeding season were in the

main restricted to pairing with that season's fledglings. As pair bonds were stable and life-long, if an unpaired adult did not find a mate at the start of the season, it might not breed the next season.

(iv) Parental care of fledglings

The distribution of sampling among different years and pairs is shown in Table 23. Numbers in brackets indicate the number of pairs sampled once or twice. The others were sampled about the same number of times each. Nearly all of the sampling was done during the 1983/84 season.

Table 23 Sampling post fledgling parental care

	First clutch		Second clutch	
	non-helper	helper	non-helper	helper
N Pairs	5(+3)	2	5(+1)	1
N watches	46	18	48	32

There was no significant difference between feeders in the average size of food items fed to fledglings (Table 24).

Table 24 Size of food items fed to young after fledging

(averages, standard deviations and sample sizes)

	First clutch		Second clutch	
	non helper	helper	non helper	helper
male parent	3.3,1.3,193	3.8,1.2,24	3.4,1.0,104	3.1,0.9,41
female "	3.3,1.6,85	3.8,1.2,46	2.9,1.0,104	3.1,0.8,41
helpers	-	3.8,1.2,46	-	3.1,0.9,29

The preferences for types of food items taken by feeders were similar across categories, supporting the earlier evidence that there were no differences between feeders in preferred prey (Table 25).

Table 25 Frequency of identified food items for each feeder (percentage of total for feeder shown)

	Moths			Caterpillars			Spiders			Wetas		
A. First clutch	M	F	H	M	F	H	M	F	H	M	F	H
Non helper	87	31	-	61	15	-	2	1	-	0	2	-
%	58	63	-	41	31	-	1	2	-	0	4	-
Helper	10	8	8	6	3	4	0	0	0	0	1	0
%	62	66	75	38	25	25	-	-	-	-	8	-
B. Second clutch												
Non helper	44	31	-	13	8	-	2	4	-	2	0	-
%	72	72	-	21	19	-	3.5	9	-	3.5	-	-
Helper	14	17	2	3	2	1	1	4	0	0	0	0
%	78	74	-	17	9	-	5	17	-	-	-	-

Feeders: M = male parent, F = female parent, H = helpers

Male parents delivered more food items to each offspring per hour than females (Figure 3-12). The differences were tested using one tailed Mann Whitney U tests (Table 26).

Table 26 Comparisons of food delivery rates of feeders during the post-fledging period (hypotheses shown: Ho = null hypothesis, Hi = alternative hypothesis)

A. First Clutch Broods		
Hypotheses	U value	P
Non helper		
Ho: M = F, Hi: M > F	1946	<0.01
Helper		
Ho: M = F, Hi: M > F	251	<0.01
Ho: H = F, Hi: H > F	260	<0.01
Ho: M = H, Hi: M =/ H	203(two tail)	>0.05(NS)
Parental comparisons: non helper(NH) versus helper(H) broods		
Ho: M-NH = M-H, Hi: M-NH > M-H	772	<0.01
Ho: F-NH = F-H, Hi: F-NH > F-H	550	<0.05
Ho: T-NH = T-H, Hi: T-NH =/T-H	491(two tail)	>0.05(NS)
B. Second Clutches		
Non helper		
Ho: M = F, Hi: M > F	1975	<0.01
Helper		
Ho: M = F, Hi: M =/F	586	>0.05(NS)
Ho: M = H, Hi: M > H	724	<0.01
Ho: F = H, Hi: F > H	662	<0.05
Parental comparisons: non helper versus helper broods		
Ho: M-NH = M-H, Hi: M-NH > M-H	1293	<0.01
Hi: F-NH = F-H, Hi: F-NH =/F-H	828	>0.05(NS)
Ho: T-NH = T-H, Hi: T-NH =/T-H	828	>0.05(NS)

note: M = male, F = female, T = total, =/ not equal

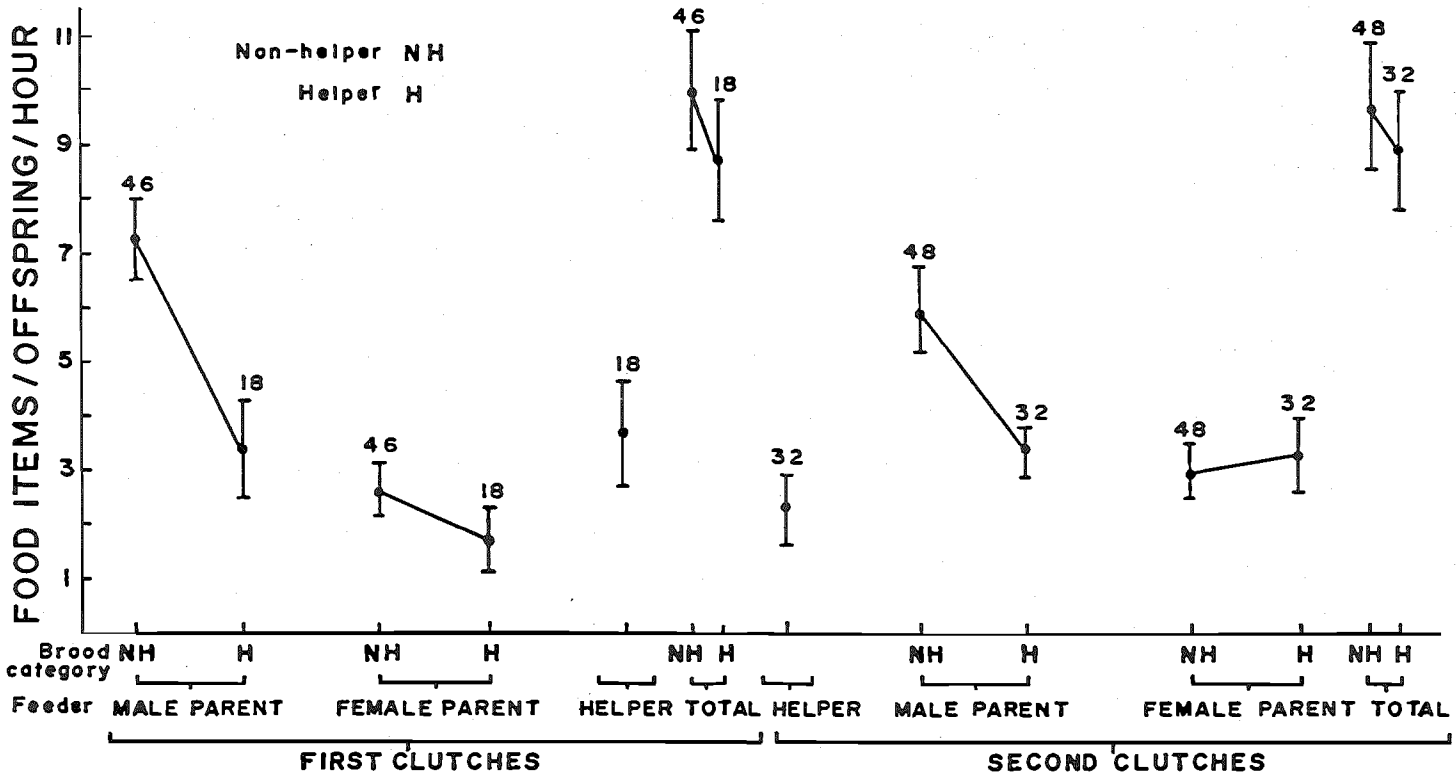


Figure 3–12 Average feeding rates at fledged first and second broods

(95% confidence intervals, sample sizes)

The comparisons illustrated in Figure 3-12 have been tested statistically in Table 26 above. As suggested by Figure 3-12 the male parent contributes significantly more food items per hour to each offspring than the female in all brood categories except second clutch helper broods. Similarly, the helpers contributed significantly more than the female parents in first and second clutch helper broods. The helper contribution did not significantly alter the total amount of food fed to offspring from helper broods suggesting that parents of "helped" broods fed young less than parents of non helper broods. There were no significant differences between the amount of food brought by female parents of second clutch non helper and helper broods, but there was a significant reduction for males (Table 26). Thus the male parents of first and second clutch broods experienced the greater degree of relief from the helper presence (Figure 3-13).

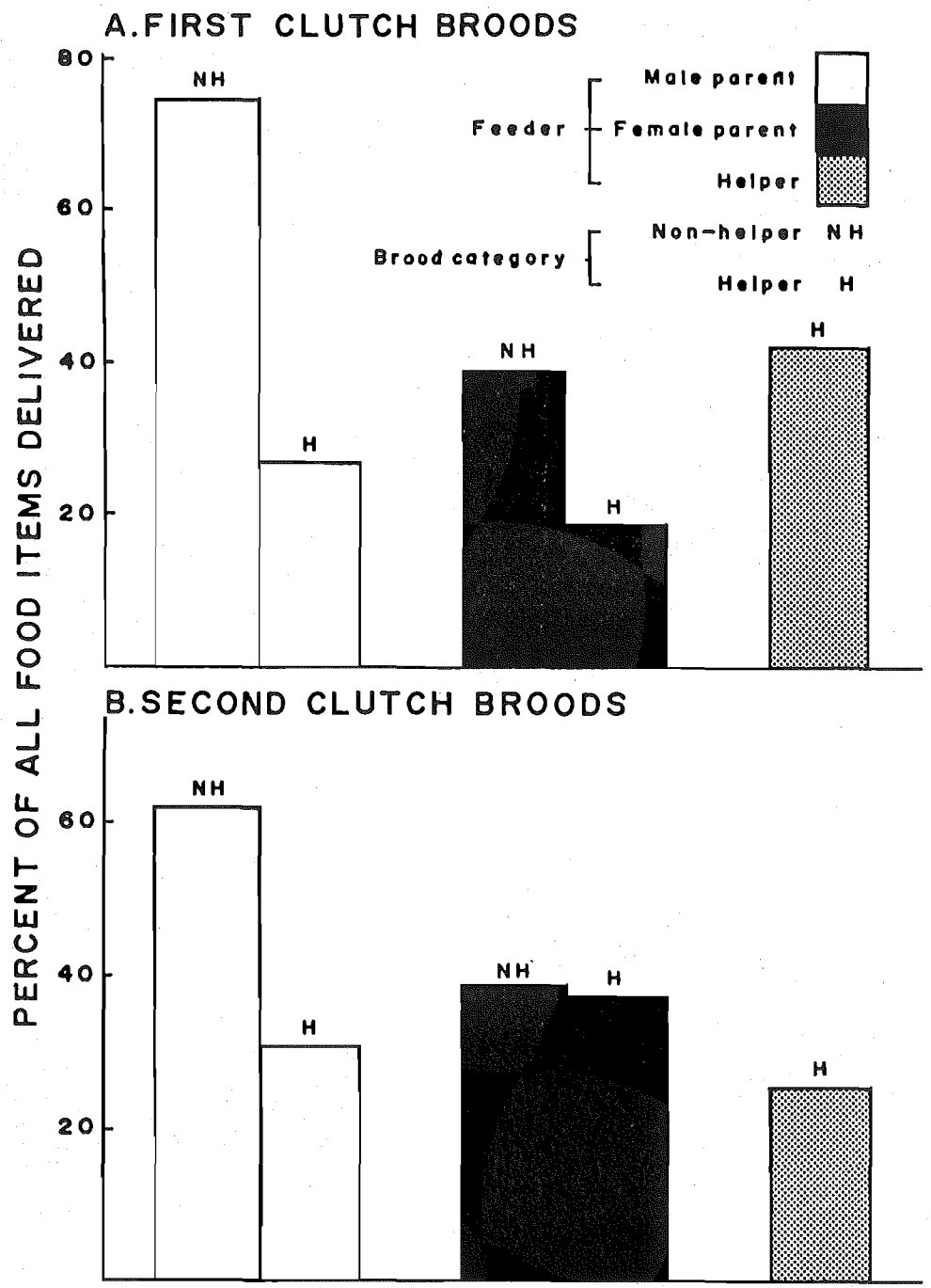


Figure 3-13 Proportion of food delivered by feeders of fledged first and second broods

D. DISCUSSION

1.Parental care

A.Feeding rate:

(i) non-helper nests

That male Riflemen fed young on average about one and a half times more often than the female during the first and second clutch nestling and post-fledging periods is exceptional for a passerine (Kendeigh 1952). Other studies of division of labour in altricial passerines (eg Smith 1978) have shown that male and female parents feed nestlings at similar rates.

The male Rifleman's major contribution to feeding the offspring during the energetically most demanding phase of the breeding cycle (Ricklefs 1974) is consistent with the main hypothesis of the thesis which predicted a highly cooperative parental care system because Riflemen are energetically constrained by their small size. As the feeding rate increased with the age of the nestlings the differential between the parents was remarkably consistent except, in the last four days of the second clutch nestling periods when the male's feeding rate dropped more than the female's. The saving in energy over the first clutch nestling and post-fledging periods probably enabled the female to cope with the demands of laying the second clutch which occurred while the fledglings were still dependant.

Considering the time potentially required to gain condition for second clutch oogenesis, it was postulated that females might compensate by reducing their contribution towards the end of the first clutch nestling period. However, no reduction occurred, possibly due to an increased availability of food at this time of the year and/or energy demands being less as the average second clutch was 0.6 egg smaller than the average

first clutches (section one).

Rifleman parents feeding fledglings did not demonstrate any preferential feeding of individuals. Hence differences in parental effort that could have arisen from parents feeding sub-groups of young of different sizes did not occur. However, parents of some Kowhai Bush passerines (eg. Grey Warbler, Gill 1980a and Robins, Powlesland 1983) and other passerines (eg. Song Sparrows Melospiza melodia , Smith 1978) discriminate in feeding particular offspring.

Considering (i) the male parent contributed so much of the parental effort over the breeding cycle and (ii) the protracted nature of the Rifleman breeding cycle (approximatly 104 days), the male's contribution could have been essential to enable rearing two broods in the time available, when food supply was adequate to feed offspring and afterwards to meet the demands of moulting. This scenario would apply to most breeding pairs as only 15% of first clutches had received aid from "regular" helpers.

(ii) helper broods

One feature of Rifleman cooperative breeding was that the frequency of occurrence of "regularly" helped second clutch nests was much smaller than the occurrence of regularly helped first clutches. Most "regular" helpers were unpaired adults which subsequently paired after the nest fledged. With these birds removed from eligibility as helpers, fewer were available to help second clutches. The paucity of second clutch "regular" helper nests precluded adequate statistical comparisons of parental care at helper as compared with non helper nests. The two examples of second clutch regular helper nests involved (i) an adult female helping its daughter, and offspring from the first clutch of that season helping regularly and (ii) a male adult of unknown background.

The behaviour of some casual helpers towards unpaired females seemed typical of bachelor males attempting to acquire a mate. If courtship-feeding included a pair bonding function then the observed soliciting behaviour and occasional feeding could be interpreted as consistent with the hypothesis that helpers are attempting to acquire mates. However, it should be noted that male casual and regular helpers probably fed male offspring in the nest and were seen to do so during the post fledging period. Thus apart fom the examples of soliciting behaviour of "casuals", there was no preferential behaviour of helpers towards a sex during the post fledging period.

The general absence of regular helpers recorded in the pilot study area correlated with an absence of unpaired adults at the start of the breeding season. The main study area was much larger than the pilot study area (approximately 80 ha as compared to 6 ha) and was only separated from another 80 ha block of forest by a 20m wide stream bed. Despite the difference in the size of the study areas, the number of breeding pairs discovered in any season was about the same in both areas ($n = 12 - 14$). The larger area of bush that the main study population occupied probably provided more room for unpaired individuals as well as immigrants from the nearby large area of bush. However, the pilot study area's small size and greater isolation (approximately 200m from the nearest large area of bush) probably could not support extra birds.

The increase in the number of casual helpers during the second clutch nestling periods in both study areas was due to the number of unpaired juveniles from the first brood of the season helping at their parents' nest. It is hard to compare the incidence of cooperative breeding in this study with others because of the different modes of helper behaviour. Few studies differentiate between types of helpers. If the comparison of incidence is limited to the number of "regular" helpers among Rifleman then

it appears that the incidence of helping was comparatively low.

Birkhead (1981) studied cooperative breeding in the Dunnock (Prunella modularis) in Great Britain. This bird was introduced into New Zealand from Britain early in the century and occurs at Kowhai Bush. Birkhead's study revealed that 38% of his population consisted of territories with two males and one female. Thomas' (1979) study on the White Bearded Flycatcher (Conopias inornata) showed that two thirds of territories studied had one helper. Another well documented long term study on a large passerine, the Florida Scrub Jay (Aphelocoma coerulescens) showed that about 50% of pairs were helped (Woolfenden, 1975). The observed 8% and 4% regular helping incidence at Riflemen first and second clutches suggests that cooperative breeding is not a significant factor in the Rifleman breeding system and not a contingency that a breeding pair can rely on.

Helping was probably facilitated by the lack of strong territorial behaviour. This aspect is discussed in section five. Despite the subjective nature of describing the degree of "territoriality" it was obvious that Riflemen did not spend as much time defending territory as did other kowhai Bush passerines such as Brown Creepers and Grey Warblers. Hence there was a high degree of tolerance of conspecifics in a breeding pair's territory, even about the nest. Lack of territorial aggression would account for some of the helpers being originally neighbours.

B. Brooding

Supplying parental heat to nestlings of altricial birds is necessary in the early stages because they are ectothermic (Welty 1975). In the absence of research on the energetic cost of brooding it seems logical that it would be "less expensive" than incubating as the hatchling's

thermogenesis must be more than the embryo's. As incubating is the least costly form of parental care (see section two) and attentiveness during brooding is much less than during incubation, then any differences between parents due to the male alleviating the female's energetic burden should be minimal. This is borne out by each parent spending about the same time brooding. Brooding ceased after twelve days by which time Rifleman nestlings were presumably homeothermic. This is within the interval for passerines quoted by Ricklefs (1978).

C. Food size

The similarity in the size and type of food items fed to young for parents of each nest category confirms the observation that the foraging methods of males and females were similar. There does not seem to be any explanation for the parents at non-helper nests (first clutches) feeding significantly larger food items than those at helper nests. As parents of a given nest category fed similar sized and types of food items, the comparisons of parental effort was simplified because the amount of energy outlayed gathering the "average" food item for each was probably the same. Howe (1978) also found parents fed similar sizes and types of food items in the Common Grackle (Quisculus quiscula) and that there was no significant difference in the size or type of food fed to male and female offspring.

2. Cooperative breeding

A. Disadvantages of helping to parents:

Helpers could conceivably advertise the nest more than parents feeding young by themselves. However, the sound of begging young could be heard by the author from about 50 metres away in ideal conditions so the sight of

extra birds was unlikely to be significant as a cue to predators.

Competition for females could have disadvantaged the alpha male. In case #2 the helper bred the same year with the alpha male's female after the alpha male disappeared. However, there was no sign that helpers were trying to oust alpha males. Acquisition of territory has been invoked as a motivation for helpers in other species (Brown 1978). But the boundaries of Rifleman territories were never well defined and in the main study area, where most regular helping occurred, there appeared to be large areas of bush (with nest boxes) which were unoccupied.

Perhaps the most significant (and hardest to assess) potential disadvantage to parents is the risk of cuckoldry to the alpha male. The few observations of interactions by unpaired male helpers towards females seem to indicate that the adult helper males were sexually active. Sperm may be added to the sperm-host gland and can result in sperm competition and subsequent fertilisation of eggs. However, multiple paternity is a much more likely outcome of cuckoldry than is single male paternity (Burns et. al. 1980 in Alatalo et. al. 1984).

Alatalo et. al. (1984) showed that cuckoldry occurs in at least two passerines, the Collared and Pied Flycatchers, where there was a frequency of 24% multiple paternity within broods, probably due to the polyterritorial behaviour of males.

Riflemen alpha males may have avoided cuckoldry by only allowing helping to start during the nestling period. Similarly, helper behaviour in Florida Scrub Jays does not occur during nest building, incubating or brooding (Woolfenden 1975). Because extra males were not present during the early phases of the nesting cycle it is thought that polygamy did not occur.

Other possible mal-effects of helpers include competition for food resources and interference with the nest (Zahavi 1974). No sign of either

was observed, although there was plenty of opportunity for the helpers to do the latter.

B. Advantages of helping to parents and offspring

During the course of the nestling periods the amount of food contributed by regular helpers increased both absolutely and as a proportion of the total food delivered to the nest. Stallcup and Woolfenden (1978) found that first year helpers at Florida Scrub Jay nests increased their contribution with the age of nestlings but decreased it over the last week. Unlike Riflemen, though, these helpers started at the first day of the nestling period. The progressive increase in the proportion of Rifleman helper contribution could have been as a consequence of habituation of the parents to the helper. Although aggressive interactions were rare, this does not remove the possibility of a progressive diminution of agonistic behaviour.

The proportion of food delivered to the nests by Rifleman helpers is comparable with the amount of food delivered by single Pygmy Nuthatch helpers (Norris 1958). At two nests helpers delivered 39% and 28% of the food. In other studies where there have been more than one helper the contribution has been much higher (eg Brown 1970, 1972). In the present study, as in other studies, one benefit to parents of helping is the reduction in the amount of energy expended feeding young (Brown 1978). Riflemen parental effort was reduced at helper nests as compared with non helper nests which is consistent with Brown's findings.

In both clutches during the nestling and post-fledging periods the male parents of helper nests generally reduced their feeding rate more than did the females. The greater advantage accruing to male parents could have allowed them more time and energy for other activities such as nest building and raising a second brood. If males were contributing parental

effort at near to their maximum, as predicted by the main hypothesis, while females were husbanding resources for later egglaying or recouperating from egglaying, then it would stand to reason that the male parents would benefit most from helper presence. Because the male benefited most, it was not expected that females of helped first broods would lay second clutches earlier. Also, the number of pairs studied was too small to make comparisons.

Although the parents benefited from helper care, the offspring did not, as the feeding rates at helped and non helped broods were not significantly different. The similarity in feeding rates has been found to be the case with other cooperatively breeding species and was further evidenced by there being no significant differences in the fledging weights of offspring from helped and non-helped broods (section four).

C. Advantages of helping to helpers

An unpaired male Rifleman has a high imperative to gain a mate at the start of the season. This imperative must be particularly acute given the relatively short reproductive life span of a male (see section four). If a male Rifleman finds itself unpaired at the start of the breeding season there are three courses of action it can take: (i) it can remain uninterested in breeding pairs and pair with what females are left over late in the season, and then breed the following season; (ii) it can become a "casual" helper visiting various nests and taking advantage of any circumstantial opportunity to gain either a widowed adult female or a juvenile close to independence and (iii) it can select one nest and establish itself as an integral part of the family unit, thus removing the hit-and-miss aspect of option (ii). Option three would probably avoid the problem of aggression from parents and would ensure a "first option" on any female offspring. This latter factor might be particularly important if

one considers that by feeding juveniles during the post-fledging period, the helper probably establishes pair bonds with potential mates. An apparent disadvantage of selecting option three is the outlay of energy in becoming a "regular" helper.

Brown (1978) and Emlen (1978) have discussed the possible costs of helping to helpers. Their reviews of research and other literature reveal little evidence of there being an energetic cost to helping. Feeding young is one of the most energetically expensive forms of parental behaviour (Ricklefs 1974), thus it seems likely that there are at least two costs to helpers : an energetic outlay for foraging, and forfeiting food which might otherwise have been eaten.

Other possible costs include an increased risk of predation by associating with a nest, and forfeiting the opportunity to breed. However, when the sex ratios differed from unity at the start of the breeding seasons, there were more males than females. Hence for male helpers, forfeiting breeding was unlikely to have been significant. The significant consideration in assessing "cost" to a helper is whether helping entails loss of fitness, i.e. future reproductive ability. Assessing fitness was outside the scope of this study. Considering the rate helpers fed offspring, there seems little doubt helping costed energy. However, at least for some helpers observed in this study, their acquiring mates could be interpreted as increasing fitness which would have offset their energetic outlay.

One of the most striking aspects of the Rifleman cooperative breeding system was the apparent lack of relatedness of regular helpers to parents except in a few cases. As the populations were only studied over a short time the pedigrees of individual birds were not well known. Hence there may have been a closer relationship between more of the helpers and parents than was thought. Inbreeding could have increased the average relatedness

of individuals in the population. The two instances of incestuous breeding (father-daughter) that occurred may not reflect the actual number of relatives that bred. Juveniles usually dispersed into neighbouring bush from their natal territory before they were one year old and hence would not have been able to discriminate between relatives when forming pair-bonds.

The number of immigrants into the pilot population over the four years of study was small (see section four). The number of immigrants that paired, established a territory and bred, were probably even fewer. Further, the pilot population (twelve breeding pairs) most probably originated from a much smaller number of pairs whose offspring spread through the available habitat. Insular populations such as the two studied might display quite a significant amount of inbreeding over a long period of time. If this was the case, there might have been a closer relationship between helpers and parents than was apparent, especially given that most new breeding positions in the population were filled with "local" recruits.

Kin selection has been proposed to explain cooperative breeding between relatives (Emlen 1978). Birds which do not breed help improve the productivity at nests of their relatives and derive benefit from reproducing their genome. Helpers probably do not improve their inclusive fitness in the Rifleman cooperative breeding system because they are not closely related to the young.

A plausable explanation for helping behaviour in Rifleman is that helpers help in order to acquire a mate, which is their reward from parents and offspring. Helpers relieve the parents of some of the energetic burden of feeding offspring, and the offspring pair with a competent forager. More than one explanation may be relevant, though, because Rifleman helping behaviour is facultative allowing the helper to opt for

either regular or casual helping. Future work could be directed at assessing the relative benefits of either helper option.

3. Conclusions:

(1) Male Rifleman parents on average performed about one and a half times more work than females while caring for young. This was consistent with the main hypothesis of the thesis which predicted a highly cooperative parental care system, especially during the energetically most demanding periods of the breeding cycle.

(2) The work done by parents and helpers was qualitatively similar.

(3) Both parents benefited from the helpers' contributions to feeding offspring but male parents benefited most.

(4) Offspring from helped nests did not fledge at significantly heavier weights than those from non helper nests.

(5) Some helpers appeared to benefit from helping behaviour by acquiring a mate.

SECTION FOUR : PARENTAL INVESTMENT, SEXUAL SIZE DIMORPHISM, SURVIVAL AND SEX RATIO

A. Introduction

Fisher (1958) related sexual size dimorphism and the primary sex ratio among sexually reproducing animals with the prediction that parental investment in each sex of offspring will be equal because their reproductive value in the next generation will be equal. His theory implied that if offspring of one sex are more costly to rear (in terms of energy and time), then natural selection will alter the primary sex ratio in favour of that sex that is least costly to raise. The theory also stated that the primary sex ratio may be altered by differential offspring mortality before independence from parents. If post-independence differential mortality occurred the primary sex ratio would "tend to be checked" by natural selection modifying that sex and improving its survival (Fisher).

The relationship between the primary sex ratio, sexual size dimorphism, parental investment and pre and post independence survival, has attracted theoretical and practical studies (eg Trivers 1972; Robertson and Biermann 1979, Biermann and Robertson 1981; Stallcup and Woolfenden 1978). One of the problems workers have faced is defining "parental investment." Trivers (1972) defined parental investment as "anything" done by the parent for the offspring that increases the offspring's chance of survival while decreasing the parent's ability to invest in other offspring. If Trivers's definition is adopted, then it is necessary to assess the cost of parental behaviour in terms of lost future fitness. But it is very difficult to measure fitness practically. Many authors have measured parental effort and use the term inter-changeably with parental investment (eg Pugesek 1983).

Reproductive effort has been defined by Tuomi et. al. (1983) as "the proportion of resources invested in reproduction." Their definition does not imply a future cost in fitness. Studies of reproductive effort have usually involved either a direct measure of the energy outlayed in reproductive behaviour or, more commonly, identifying parameters which are the product of energy outlay of parents. In measuring parental investment in each sex of offspring, Fiala (1981) used the weight of offspring to reflect differential parental investment in each sex.

In the face of the impracticability of measuring parental investment (sensu Trivers), in this study it has been assumed that a difference in weight per juvenile sex (hence a difference in parental or reproductive effort) reflects differential parental investment.

The Rifleman breeding system provides a test case for Fisher's theory because its young are sexually dimorphic in size and plumage from an early time during the period of parental care. Riflemen also provide an opportunity to investigate why sexual dimorphism occurs. Male Riflemen are unusual in that they are smaller than females, and neither sex is brightly coloured. Sexual dimorphism is usually associated with increasing polygamy and decreasing parental care (Verner and Willson 1969). The larger body size of females and extensive parental care of male Riflemen suggests a physiological function for the female's large body size.

Hypotheses tested

(i) That the primary sex ratio of Riflemen broods is unity.

(ii) That female nestlings grow at a faster rate than male nestlings.

(iii) That female nestlings weigh significantly more than male nestlings throughout the nestling period

(iv) That female nestlings are significantly larger than male nestlings in bill and tarsii dimensions throughout the nestling period.

(v) That female and male nestlings have the same chance of survival to one year of age and they have the same chance of reproduction.

(vi) That female nestlings from unisex broods will weigh significantly less than females from mixed sex broods.

(vii) That male nestlings from unisex broods will weigh significantly more than males from mixed sex broods.

B. METHODS

1. Sexing and measuring young

Newly hatched Riflemen weighed 1.0-1.2g and were extremely fragile. Therefore, only a few measurements of nestlings under the age of four days were made. Before nestlings could be sexed visually, birds were marked with a spirit ink pen on a leg or wing. Birds were sexed at 10-12 days old by plumage differences. Gray's (1969) (page 14) description of the difference was accurate for Kowhai Bush Riflemen : "The male has greenish coloured tips [on the sterno-abdominal pterylae] while the female has tips of a dusty ochre colouring". Subsequently one celluloid "AA" colour band was used to differentiate individuals. Birds were uniquely colour banded at about 18 days old (see general methods).

Nestlings were measured only in nests not being used for observational data on parental care. Weighing was done to the nearest 0.1g using a Pesola spring balance and placing a nestling in the corner of a plastic bag cut off to a convenient size and weight. Birds were measured on alternate days to minimise any disruption of parental feeding of young and consequently disruption of nestling weight gain. Nestlings were not

induced to defaecate before weighing.

The following dimensions were measured with calipers to the nearest 0.1mm after Gurr (1947): total culmen, culmen width, depth and two tarso-metatarsal lengths. One "tarsus" measure used on older birds was taken by the method Gurr (1947) described. The dimension is from behind the tibio-tarsal joint diagonally to the anterior flexure of the folded foot. However, taking this dimension was impractical with very young birds because of the difficulty of handling them. The other tarsus dimension was from the anterior flexure skin fold between the toes and the distal end of the tarsus bone to the posterior mid point of the tibio-tarsal joint.

Total culmen length was taken from the facio-cranial hinge to the tip of the culmen. Culmen width and depth were measured at the feather line or where the rictal flange joined the bill. Wing measurements were taken to the nearest 0.5mm with the wing unstraightened and not flattened. The points from which measurements were taken were from the insertion of the "bastard" wing (which correlates with the carpel joint) to the distal end of the fifth primary.

2. Hatching success

The number of eggs laid and hatched was calculated from the clutch size determined at the end of laying, minus the number of unhatched eggs left in the bottom of the nest bowl (determined when banding young due to fledge). The primary sex ratio could not be measured directly as there is no known way of sexing eggs. The mortality of hatchlings before the age when sexual dimorphism could be discerned was low and was likely to have been the same for each sex. In the absence of a method for sexing eggs it was assumed that the observed nestling sex ratio was a reliable estimate of the primary sex ratio.

3. Survival

The 15th of October, which corresponds to mid spring, was set as the anniversary date for the calculation of annual survival. A census was taken annually from 1981 to 1984 in the main study area and from 1982 to 1984 in the pilot study area. Rifleman are "noisiest" over mid spring and have usually begun nesting by then. Birds not seen during the census but seen later in the season were included in calculations of survival. Most data on survival were gathered by counting birds at nestboxes. Unpaired birds could also be counted during watches on nests as these were frequently helping to feed chicks (section three).

Systematic searches of bush adjacent to the study areas were made at each end of the breeding season in order to detect emigration. Immigration into the main study area could not be monitored because non-banded birds could have come from breeding pairs not followed the previous season. However, in the pilot study area all breeding pairs were followed and offspring banded.

C. RESULTS

1. Primary sex ratio

In the main and pilot study areas over all seasons 47% and 48% respectively of the offspring were males (Table 1). There were no significant differences in the totals of the sexes for the main study area (X^2 = 0.89, df = 1, P > 0.05) or the pilot study area (X^2 = 0.23, df = 1, P > 0.05). Yate's correction was applied to the values of X^2. Thus the primary sex ratio in the main study area was not significantly different to unity.

Table 1 Number of male and female offspring in Rifleman broods

Study area:	Main			Pilot		
	M	F	Unhatched	M	F	Unhatched
A. 1980/81						
clutch #1	25	16	7	-	-	-
clutch #2	6	4	0	-	-	-
B. 1981/82						
clutch #1	24	36	1	14	19	8
clutch #2	12	10	6	4	12	0
C. 1982/83						
clutch #1	24	35	5	27	23	8
clutch #2	14	9	2	no nests that year		
D. 1983/84						
clutch #1	25	38	8	20	15	7
clutch #2	23	23	13	9	12	6
Totals	153	171	42	74	81	29

The proportions of eggs that failed to hatch in the main and pilot study areas were 11% and 16% respectively. As eggs could not be sexed, the extreme possibility that all the unhatched eggs studied were male embryos was investigated: if all eggs contained male embryos the chi-square value comparing the two population's primary sex ratios (X^2 = 1.44 and 2.40 respectively) would still not be significant (P > 0.05).

Similarly, if up to half the unhatched eggs of the main study population were female embryos which died, the primary sex ratio would not be significantly different from unity (X^2 = 4.18, P > 0.05). In the event of half or more (n > = 21) being female embryos the difference would be significant at the 5% level. If two thirds of the unhatched eggs observed from the pilot study population were dead female embryos the primary sex ratio would not be significantly different (X^2 = 3.80, P > 0.05) from unity.

It is highly unlikely that the unhatched eggs involved the above proportions of dead embryos of either sex. Some unhatched eggs were broken and there was no evidence of dead full-term or part-term embryos. It seems, therefore, that the majority of unhatched eggs were infertile and hence the presence of embryo mortality would not affect the conclusion that the primary sex ratio was unity.

Once eggs hatched mortality due to other factors apart from predation was very low. Only three hatched nestlings died from other causes. Four nestlings died before the age of four days during handling. The broods from which these nestlings came were not counted in the sex ratio calculations. Predation was the main cause of mortality (> 90%). No nests were partially preyed on as the main predators (Stoat, Mustela erminea and Ship rat, Rattus rattus) always completely destroyed nests and so precluded them from consideration.

2. Sexual dimorphism of Riflemen

A. Physical development of nestlings

Days 1-6. Unlike Grey Warblers (Gill 1980a), Riflemen hatched with no natal down and none developed during the nestling period. They were feeble and only just able to lift their heads and beg with a soft high pitched peeping. After four days their light pink skin had darkened along

the feather tracts. By the sixth day the feather tracts were well defined and the eyes were partially open.

Days 7-12. By the seventh day the nestlings could crawl around and were generally more active. Papillae were only emerging from the primary pterylae while the rest were about to erupt through the skin surface. By day twelve all the pinnae had emerged from the skin and all the feathers had started to erupt except on the capital tract. The feathers most advanced were those of the sterno-abdominal tracts and the spinal tract. The spinal tract feathers could be used to differentiate the sexes. The eyes by then were completely open and vocalising was loud when the nestlings begged for food.

Days 13-24: At 13 days the size and especially the plumage differences between the sexes were usually apparent and was certainly established by 15 days.

B. Nestling weight

Female nestlings attained significantly heavier weights than males over most of the nestling period (Figure 4-1, Table 2).

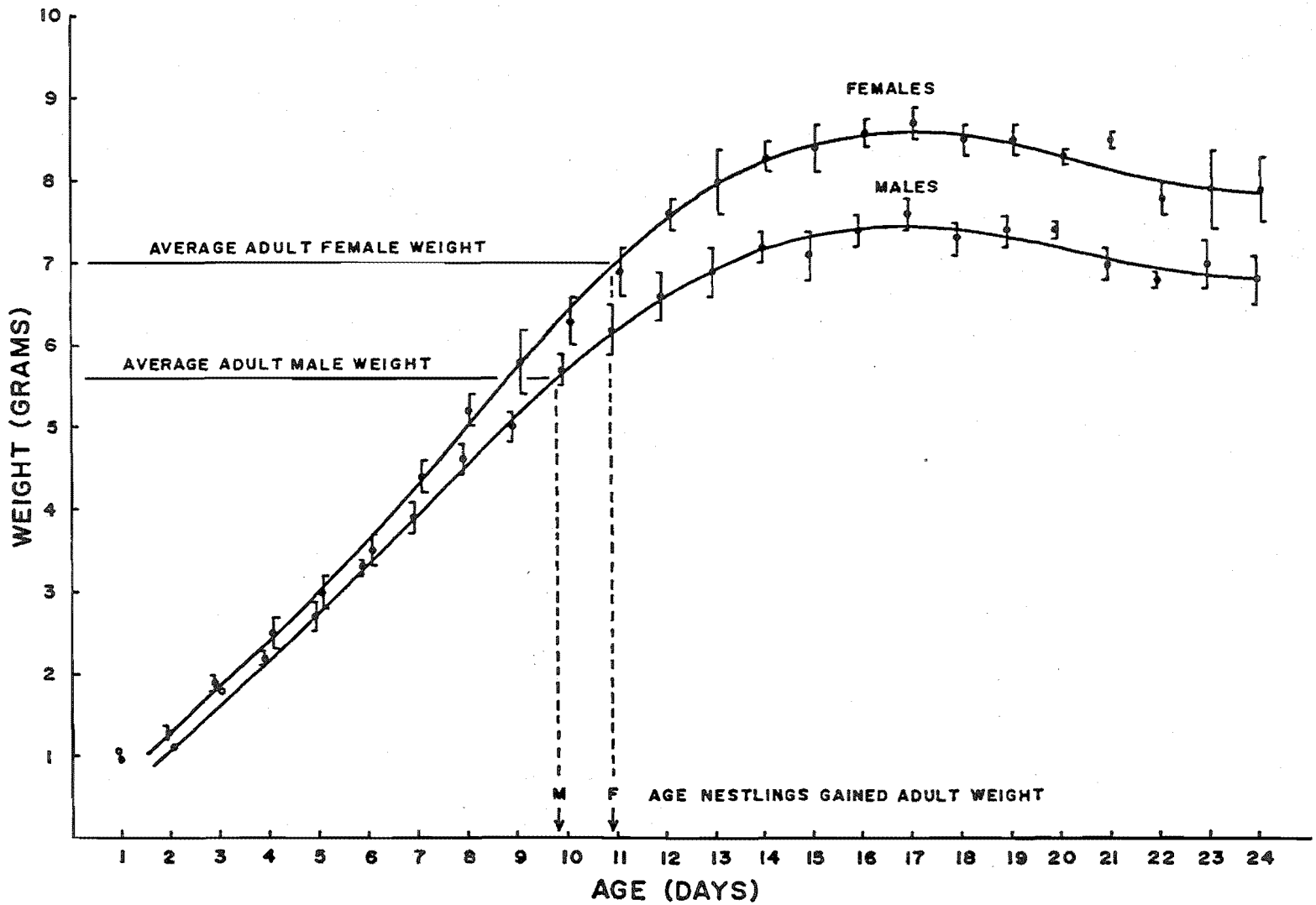


Figure 4-1 Average weight-age curves for Riflemen nestlings (95% confidence intervals indicated).

Table 2 Comparison of average male and female nestling weights with T test

Day	Males			Females			
	Wt	SD	N	Wt	SD	N	T
7	3.9	0.5	22	4.4	0.5	19	3.19*
8	4.6	0.6	37	5.2	0.7	32	3.68*
9	5.0	0.6	22	5.8	0.8	19	3.65*
10	5.7	0.6	39	6.3	0.9	38	3.43*
11	6.2	0.6	19	6.9	0.6	13	3.24*
12	6.6	0.8	37	7.6	0.7	35	5.63*
13	6.9	0.7	25	8.0	0.9	24	4.79*
14	7.2	0.7	40	8.3	0.6	36	7.31*
15	7.1	0.8	26	8.4	0.8	28	6.00*
16	7.4	0.7	39	8.6	0.6	32	7.66*
17	7.6	0.4	23	8.7	0.5	18	7.83*
18	7.3	0.6	37	8.5	0.6	33	8.35*
19	7.4	0.4	15	8.5	0.5	18	6.88*
20	7.4	0.4	57	8.3	0.6	62	9.54*
21	7.0	0.6	52	8.5	0.4	40	14.35*
22	6.8	0.4	31	7.8	0.6	38	8.27*

* : $P < 0.005$

The growth curves of males and females were non-sigmoid as there was a decline in weight after the asymptote which was reached after about the 17th day. At the asymptote females weighed on average 1.1g (14.5%) more than males. As the growth curves were non-sigmoidal no attempt was made to fit to the data any of the equations describing growth mentioned by Ricklefs (1968). The growth curve of Grey Warbler nestlings was also non-sigmoid (Gill 1980a) and showed a recession in weight. Hence both Riflemen and Grey Warblers differ from most passerines whose growth-curves of weight are usually sigmoidal (Ricklefs 1967; 1968).

The average amount of recession (maximum weight minus final weight) was 0.7g for males and females which corresponds to 9% and 14% respectively of maximum nestling weights. In contrast a 4.2% recession was found in Grey Warblers (Gill 1980a). The average maximum weights of male and female nestlings differed significantly from their average weights at 22 days old (t tests: $t = 7.27$, $P < 0.001$; $t = 5.51$, $P < 0.001$, respectively) indicating that a real decline had occurred.

In order to help assess the relative cost of nestling sexual dimorphism to the parents, regressions of weight on age were conducted for male and female data between the ages of 3 days and 12 days. During this period the greatest increase in weight occurred (Figure 4-1). Regression analyses were performed using 45 and 51 different male and female nestlings respectively. Birds in the right age group were selected randomly and only used once in calculations. Data were taken from different nests from all seasons in which growth data were collected. The regressions were significant for males and females (F test, $P < 0.05$; Table 3).

Table 3 Analysis of covariance table for nestling weight between days 3 to 12 inclusive

					Regression		Residual		
	N	Slope	F	Yint	SS	DF	SS	DF	R2
Source									
Males	45	0.59	378	-0.21	127.8	1	145.40	43	0.90
Females	51	0.58	162	0.32	122.5	1	366.99	49	0.77
Pooled							51.53	93	
Common							51.54	94	
Total	96	0.59	419.85	0.04	254.1	1	56.89	94	0.82

A test for coincidental regressions was significant ($F = 4.785$, $P < 0.05$, $df = 2,92$) indicating that it was highly unlikely that the male and female lines were the same. The test for the equality of the slopes was not significant while the equality of the elevations was significantly different ($F = 9.658$, $P < 0.005$, $df = 1,93$). Hence it was concluded that there was no significant difference between males and females in the rate of weight gain but that the females were consistently gaining a larger absolute amount of weight per day between days 3 to 12. The latter conclusion supports the notion that females are receiving more food than males and that the size sexual dimorphism occurs from an early age onwards.

C. Nestling culmen and tarsus

Bill length and tarso-metatarsal length were followed throughout the nestling period. The females were usually larger than the males, but there were no consistent statistically significant differences (Table 4, Figures 4-2 and 4-3).

Table 4 Comparisons of average male and female nestling culmen and tarsus length with T test

A. Culmen	Male			Female			
Day	X	SD	N	X	SD	N	T
1	3.20	-	1	3.85	-	2	-
2	4.00	-	7	4.35	-	2	-
3	4.61	-	8	4.23	-	6	-
4	4.75	0.58	17	5.02	0.57	12	NS
5	5.33	0.51	12	5.68	0.40	9	NS
6	5.87	0.55	22	6.31	0.51	15	NS
7	6.32	0.47	20	6.51	0.53	11	NS
8	7.01	0.41	33	7.34	0.50	27	NS
9	7.32	0.44	22	7.65	0.39	18	NS
10	7.64	0.40	39	8.04	0.66	37	3.16*
11	7.86	0.44	19	8.33	0.55	13	NS
12	8.38	0.51	36	8.77	0.57	33	3.00*
13	8.58	0.60	25	8.93	0.76	23	NS
14	8.96	0.54	36	9.15	1.72	34	NS
15	9.10	0.57	22	9.43	0.67	27	NS
16	9.20	0.68	41	9.89	0.45	31	5.19*
17	9.38	0.54	24	9.76	0.53	18	NS
18	9.64	0.65	40	10.23	0.48	31	4.41*
19	9.36	1.20	13	9.68	0.56	16	NS
20	10.05	0.55	54	10.50	0.70	70	4.02*
21	9.95	0.60	24	10.70	0.60	27	4.46*
22	10.60	0.90	11	11.20	0.95	15	NS
23	10.10	0.45	9	10.10	0.60	10	NS
24	10.40	-	5	10.60	-	2	-

Table 4B.Tarsus

1	5.00	-	1	5.10	-	2	-
2	5.70	0.52	10	5.55	-	2	-
3	7.16	-	8	6.26	-	5	-
4	6.90	1.35	14	7.80	0.31	9	NS
5	8.71	0.90	9	9.00	-	6	-
6	9.27	1.69	22	10.40	0.94	17	NS
7	11.28	0.98	20	11.76	0.88	11	NS
8	12.81	1.39	33	13.21	1.17	26	NS
9	13.83	0.96	22	14.69	1.43	18	NS
10	15.25	0.78	38	15.33	2.85	35	NS
11	16.38	0.78	19	16.73	1.02	13	NS
12	17.22	0.77	35	17.61	0.98	33	NS
13	17.62	1.15	24	17.77	1.48	25	NS
14	17.94	0.78	36	18.44	0.87	34	NS
15	18.21	0.98	22	18.87	1.28	25	NS
16	18.35	0.81	40	19.21	0.78	34	4.62*
17	17.22	4.18	19	19.10	0.97	15	NS
18	18.61	0.83	38	19.34	0.75	33	3.87*
19	17.83	0.47	9	19.21	0.64	16	5.65*
20	18.38	0.63	54	19.14	0.59	58	6.57*
21	18.10	0.55	26	18.77	1.86	30	NS
22	19.76	-	4	19.95	0.67	12	-
23	18.68	-	6	19.42	0.42	9	-
24	18.48	-	3	18.87	-	2	-

* - denotes significance at the 5% level

A similar pattern occurred with bill width of nestlings at 20 and 21 days of age (Table 5).

Table 5 Bill width and depth of 20 and 21 day old nestlings

A. Bill Width:

	Male			Female			
	X	SD	N	X	SD	N	T
Day 20	2.80	0.19	26	2.91	0.26	31	1.78 NS
Day 21	2.73	0.21	18	2.87	0.19	16	2.04 NS

B. Bill Depth:

Day 20	2.23	0.16	39	2.34	0.12	53	3.42 *
Day 21	2.21	0.12	28	2.33	0.12	26	3.00 *

* denotes significance at 2.5% level

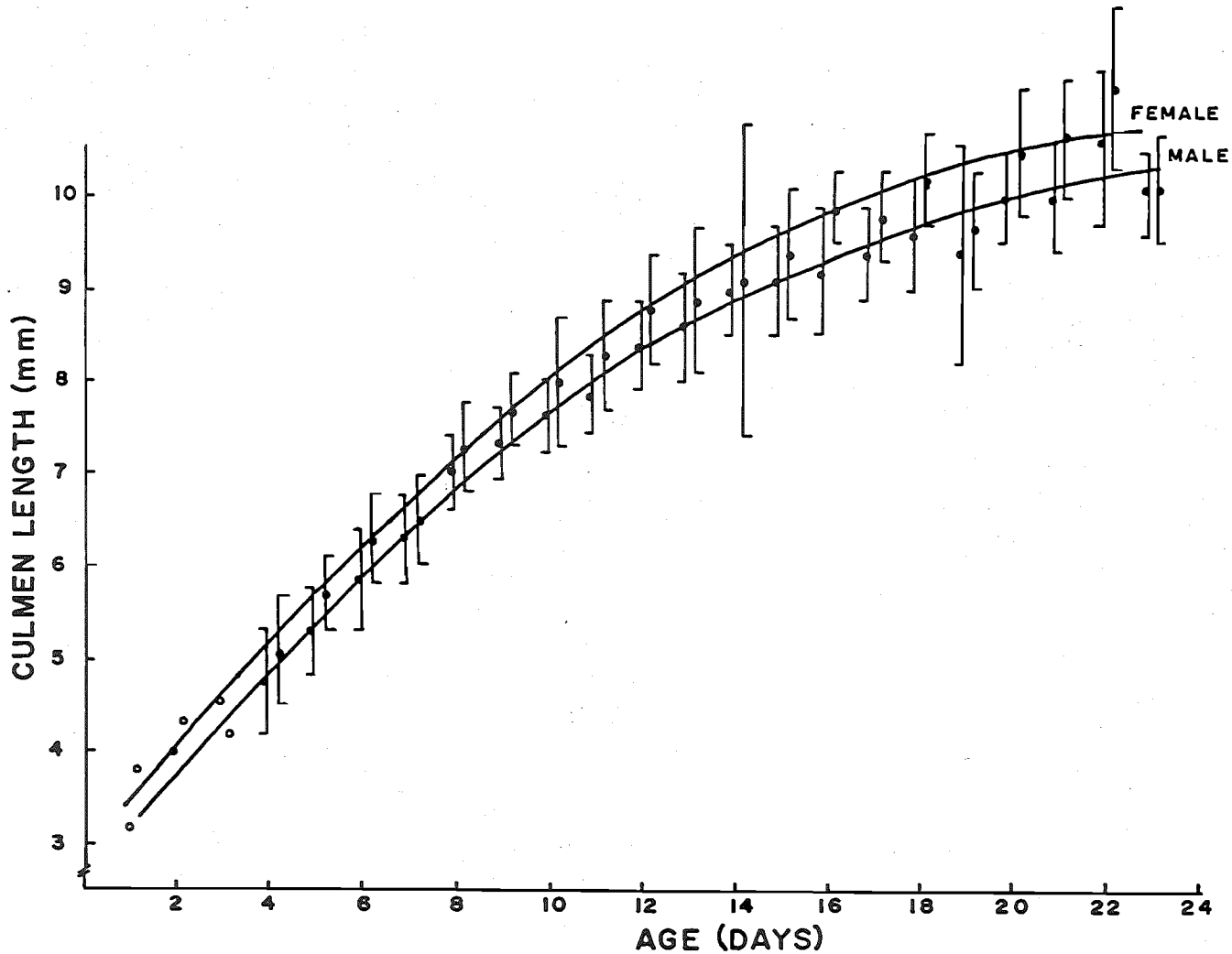


Figure 4-2 Average culmen growth curves for first clutch Riflemen nestlings (± 1 SD).

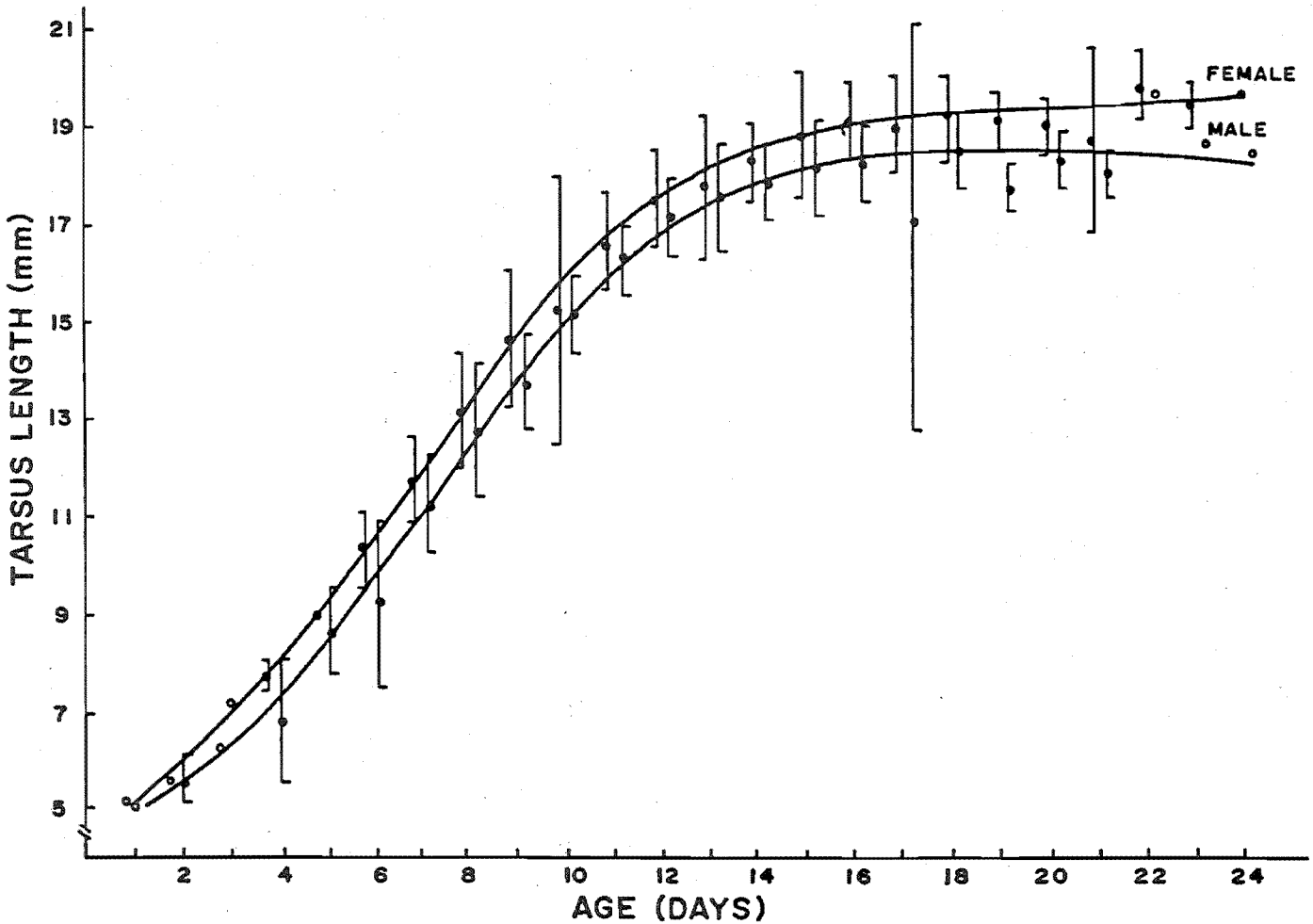


Figure 4-3 Average tarsii growth curves of first clutch Riflemen nestlings (± 1 SD).

However, female bill depths at these ages were significantly deeper than male bill depths. Overall, there was a pattern of female nestlings being larger than males although the only consistent difference was that females weighed more than males.

D. Differential maturation of male and female nestlings

Male nestlings reached the average adult weight one day earlier than females (Figure 4-1). However, neither adult culmen length nor male tarsus is reached by juveniles before they fledge. Hence it is not possible to gauge whether there is any differential maturation.

E. Second clutch nestling sexual dimorphism

Data were taken at banding which was usually done at 20 or 21 days of age. The brood sizes from which these data were taken were either three or four and from all seasons studied. Generally, female second clutch nestlings were significantly larger than males (Table 6).

Table 6 Dimensions of male and female second clutch nestlings at days 20 and 21

	Male			Female			
	X	SD	N	X	SD	N	T
Bill width	2.77	0.14	13	2.96	0.19	9	NS
Bill depth	2.21	0.11	20	2.34	0.06	17	5.64*
Bill length	9.84	0.56	22	10.54	0.42	17	4.28*
Tarsus #1	18.14	0.57	23	19.00	0.78	17	3.86*
Tarsus #2	19.11	0.50	21	19.92	0.70	17	NS
Weight	7.1	0.4	25	8.5	0.5	21	10.28**

* denotes $P < 0.05$, ** denotes $P < 0.001$

The general patterns of significantly heavier female weights after the first week of the first clutch nestling period, faster (though not statistically significant) rate of growth from days 3 till 12 and larger female averages of morphological dimensions especially by the late stages

of the nestling period, suggest that female nestlings are likely to cost more to raise than male nestlings.

F. Comparisons of mixed sex and unisex broods.

If females were more costly to rear than males, then females from unisex broods may have been expected to weigh less than females from mixed sex broods because of the extra demands on the parents. Also males from unisex broods might have weighed more than those in mixed sex broods because of the reduced demands on parents.

For the following comparisons it was necessary to pool data from broods of 4 and 5 nestlings to make up adequate sample sizes. To justify pooling these data male and female weights from mixed sex broods of four and five, including those for helper and non-helper nests, were compared. There were no significant differences (Table 7A).

Table 7 Nestling weights at 20 days of males and females

	Males			Females		
A. Brood size 4/5:	X	SD	N	X	SD	N
Brood size = 4	7.3	0.35	50	8.2	0.59	54
Brood size = 5	7.3	0.52	36	8.2	0.58	41
t test		NS			NS	
B. Offspring from mixed sex/unisex broods:						
Mixed sex	7.3	0.41	75	8.4	0.46	65
Unisex	7.6	0.27	8	7.9	0.57	18
t test		NS		t = 3.89, P < 0.025		
C. Offspring from helper/non-helper broods (sizes 3-5 combined):						
Helper	7.4	0.51	17	8.5	0.35	22
Non-helper	7.3	0.39	97	8.3	0.61	102
t test		NS			NS	

The significantly heavier weights of 18 female nestlings from the four unisex broods studied confirm the hypothesis that females are more costly to raise (Table 7B). However, the corresponding comparison of male nestlings was not significant although the difference in the average weights was in the predicted direction. The absence of a difference may

be attributable to small sample size (two broods, 8 young).

These comparisons, therefore, generally support the contention that females were more "costly" to raise. The comparisons between mixed sex and unisex broods were not complicated by any of the broods studied being "regularly" helped. The comparison of nestlings from broods with and without helpers indicates that there was no significant increase in late nestling weights (taken to be close to fledging weight) from helped and non-helped nests (Table 7C).

G. Sexual dimorphism in adults

The pattern of females being larger than males established during the nestling period is retained in adulthood (Table 8).

Table 8 Proportional size difference and sexual dimorphism in adult Riflemen

	Male			Female		
	X	SD	N	X	SD	N
A.Weight	5.6	0.3	33	7.0	0.7	20
	$t = 9.94$, $P < 0.001$; % difference = 25					
B.Bill length	12.22	0.62	34	13.20	0.67	20
	$t = 5.46$, $P < 0.001$; % difference = 8					
C.Bill width	2.89	0.32	34	3.28	0.37	21
	$t = 4.14$, $P < 0.001$; % difference = 13					
D.Bill depth	2.24	0.17	34	2.45	0.18	21
	$t = 4.37$, $P < 0.001$; % difference = 9					
E.Tarsus #1	19.34	0.91	30	20.02	0.75	18
	$t = 2.67$, $P < 0.01$; % difference = 4					
F.Tarsus #2	18.69	0.66	33	19.34	0.64	21
	$t = 3.56$, $P < 0.001$; % difference = 3					

3. Survival

A. Survival of juveniles

One of the theoretical assertions made by Fisher (1958) was that male and female offspring are of equal value to their parents in a sexually

reproducing species. There has since been some debate as to whether post-independance mortality can have an effect on the evolution of the primary sex ratio. In order to investigate this question, data are presented for both study populations on survival to breeding age (at least eight months), breeding frequency of offspring, and adult survival for each sex. The data from the "pilot" study population represent the whole population (excluding emigrants) because all breeding pairs were followed and nearly all birds were banded.

The survival data have not been corrected for immigration because the observed immigration was low and apparently equal for each sex. Thus the statistics mentioned here are probably slightly conservative. In the "main" study population, dispersal into the remote areas of the same patch of forest could have occurred and gone unnoticed, hence influencing results, although the number of birds involved would have been small. The survival of juveniles to four and three years of age in the main and pilot study areas respectively is shown in Table 9. These ages correspond to the number of annual censuses undertaken in each study area after the first breeding season studied. The "number at risk" are the number of birds that were studied for one to 4 years of age.

Table 9 Survival and breeding of Riflemen banded as juveniles

A.Main study population

			Males	
Age(years)	1	2	3	4
number at risk	144	100	66	29
number surviving	16	5	2	0
proportion surviving	0.11	0.05	0.03	0
number breeding	11	5	2	0
% surviving to breed	8	5	3	0
			Females	
number at risk	159	106	70	23
number surviving	30	15	6	3
proportion surviving	0.19	0.14	0.09	0.13
number breeding	26	14	6	3
% surviving to breed	16	13	9	13

Table 9B.Pilot study population

		Males		
Age(years)	1	2	3	4
number at risk	70	46	21	-
number surviving	23	10	2	-
proportion surviving	0.33	0.22	0.09	-
number breeding	10	9	2	-
% surviving to breed	14	20	9	-
		Females		
number at risk	91	54	31	-
number surviving	27	12	4	-
proportion surviving	0.30	0.22	0.13	-
number breeding	17	10	4	-
% surviving to breed	19	18	13	-

Only results for the pilot study area are graphed in Figure 4-4 as some individuals in the main study area went unrecorded. The results indicate that males and females of the four cohorts studied could expect to live to similar ages and breed a similar number of times (Table 10).

Table 10 Total number of breeding occasions of juvenile Riflemen surviving to maturity in the Pilot study area

	Male	Female	X^2	
Number of juveniles at risk	70	91	2.48	NS
Occasions juveniles bred in following yrs	21	31	1.55	NS
Proportion of juvs	0.30	0.34		

Table 10 is based on three years of observing juveniles in consecutive years. These results and those of Table 9b support the hypotheses that survival of junvenile males and females to one year, and the reproductive value of male and female offspring to parents, are the same.

B. Suvival of adults of unknown age

The survival of birds banded as adults (and hence of unknown age) until the following year is shown in Table 11. No adults were banded in the 1983/84 season in either study area and research had not begun in the pilot study area in 1980.

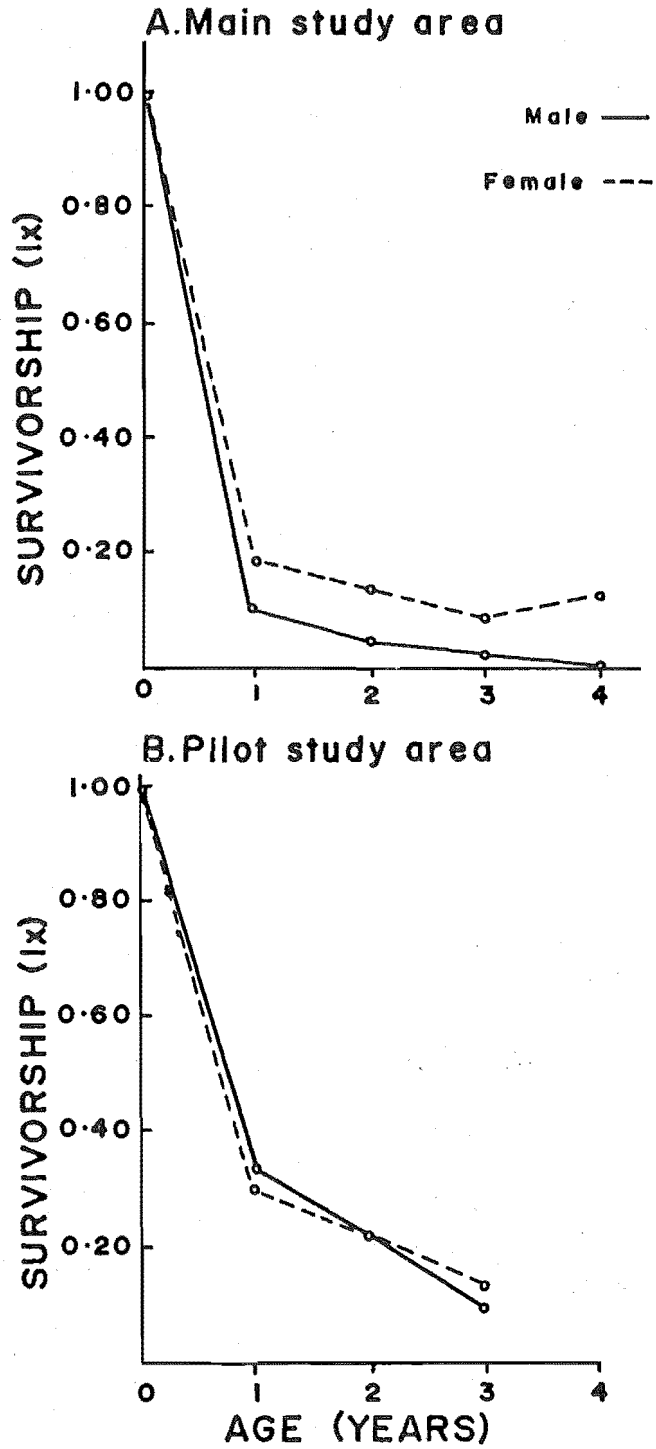


Figure 4-4 Survival of offspring in (a) the main and (b) pilot study areas.

Table 11 Survival of unknown aged adult Riflemen

A.Main study population						
Interval	1980-81		1981-82		1982-83	
Sex (M=male, F=female)	M	F	M	F	M	F
number at risk	20	14	19	13	15	5
number surviving	15	8	8	7	8	3
proportion	.75	.57	.42	.54	.53	.60
B.Pilot study population						
number at risk	no data		12	9	12	5
number surviving	-	-	9	3	8	4
proportion	-	-	.75	.33	.67	.80
C.Both populations						
number at risk	20	14	31	22	27	10
number surviving	15	8	17	10	16	7
proportion	.75	.57	.55	.45	.59	.70

The average annual adult mortality of unknown age male and female Riflemen was 37% and 43% respectively. This compares with 18.5% for Grey Warblers (Gill 1980) and 40-70% for most temperate passerines (Farner 1955). Using Gill's equation (quoted from Gibb 1961 in Gill 1980a) the average expectation for further life is 2-m/2m, where m is the annual mortality. Substituting the values for "m" for male and female Riflemen the life expectancy for adults in years is 2.2 and 1.7 respectively.

4. Emigration

Three juveniles (two female and one male) were found in forest adjacent to the main study area. The two females had left the main study area while the male had left the pilot study area. Three juveniles (two males and one female) moved from the pilot study area to the main study area, and one juvenile female and one adult male which had previously bred successfully moved from the main study area to the pilot study area. Hence all but one case of emigration involved juveniles and there was no sex bias. These results suggest that (i) similar numbers of each sex of juveniles emigrate (or disperse), (ii) adult Riflemen are sedentary and (iii) the influence of emigration on survival data is small, similar for each sex, and applies mainly to juveniles.

D. DISCUSSION

A. Is there a cost differential in parental effort in a sexually dimorphic species?

There is much debate and conflicting evidence on the question of whether sexual size dimorphism involves a cost differential in fitness to the parents. Fiala and Congdon (1983) determined from an energetic study that male Red Winged Blackbirds (Agelaius phoeniceus) cost parents more to raise than females, although proportionally the difference in the total energy assimilated by the two sexes is less than the weight difference. In Riflemen, rearing larger female nestlings, therefore, may not involve more parental effort especially as the degree of sexual dimorphism in Riflemen is much smaller than in Red Winged Blackbirds.

A consideration of patterns of maturation is necessary to establish a true difference in parental expenditure. In this study the growth curves of culmen length and tarsus length showed no differences between the sexes in the age that they attained adult dimensions. However, males reached adult weight about one day earlier than females did, suggesting that there was no obvious differential maturation present in juvenile male and female Riflemen. Also there were no consistent differences between the males and females in the variability in weight, culmen length and tarsus length during the nestling period. The greater variability in weight for a given age was interpreted by Richter (1983) as a result of the larger investment in the bigger sex being more dependent on environmental limitations such as food supply.

Even though there are too few data to determine if differential maturation existed in Rifleman, it seemed unlikely given the extremely long nestling period from which it would be expected males and females would fledge relatively mature. Furthermore, like all birds, Riflemen exhibit

determinant growth and achieve physical maturity within the period of parental care. Hence it is theoretically difficult to conceive how differential maturation could equalise parental effort.

To explain differential parental investment in the sexes in Yellow Headed Blackbirds Richter (1983) (page 166) hypothesised "that two complementary mechanisms, earlier maturation in the smaller sex and greater variability of food received in the larger sex, combine to reduce the dimorphism in costs to parents below that apparent from offspring size dimorphism". If this hypothesis is correct then one might expect the lighter sex to acheive independence earlier. No data addressing this were reported in the literature mentioned and none were gathered in this study. However, there might not be a correlation between physical maturation and the rate of acquiring behavioural skills such as foraging proficiency. For example, if female Riflemen fledged in a more mature state then they might require less post-fledging parental care.

Another explanation of differential parental investment relates to the relationship of clutch size and environmental resources. Schaffer (1974) has given a theoretical account of how environmental uncertainty of breeding success can reduce optimal brood size relative to the optimum for mean conditions. This hypothesis is supported by Merton and Westwood (1977) (page 193) who claim that "it is probable that many nidicolous and particularly passerine birds function well inside the potential energy threshold limit, so that their clutch size will be primarily geared to the number of chicks that can be effectively reared." If this reduction of brood size as a result of environmental uncertainty occurs with Riflemen, then there probably exists enough latitude in the ability of parents to outlay sufficient reproductive effort to cope with offspring whose sexes are dimorphic by a factor of 0.25 at their maximum weight.

That parents reproduce at a rate within the theoretical maximum that

the environment and the birds can sustain is contrary to Lack's (1968) hypothesis that average clutch size (assumed to equate with brood size) matches the average food supply available to the parents. Food supply was qualitatively observed to fluctuate in this study after the storm of 1983 which involved a gale of hot wind. Most of the second clutches (which existed as nests and partially laid clutches at that stage) were subsequently deserted, suggesting that parents were sensitive to food availability and that food availability was a proximate factor in breeding success.

Field evidence for brood size optimisation has been published by Nur (1984). He found a discrepancy between observed and optimal brood size and concluded that time and energy constraints may act to limit brood size during the laying period. Further, if survival probabilities (especially for offspring) are unpredictable from year to year restrained reproductive effort may be the best course to take. These conclusions are significant given that the work was done on the Blue Tit which lays one of the relatively largest clutches in the world : about 130% of female body weight. Similar constraints may be acting on Riflemen which also lay a relatively large mass of eggs.

Gill (1980a) suggested that native passerines at Kowhai Bush are constrained by food availability as evidenced by their protracted breeding cycles. Riflemen have an even more protracted breeding cycle than do Grey Warblers. It is this author's contention that a further constraint on Riflemen apart from their small size is food availability and that clutch size restraint below the theoretical maximum probably occurs. Any extra effort demanded in rearing female offspring (if it in fact occurs) is within the physiological abilities of the parents because they are working within their physiological maximum.

B. How does sexual dimorphism occur?

It is possible that "sexually dimorphic" eggs might have occurred in Riflemen as sexual dimorphism was noticed from an early age. Bimodal egg weights have been observed in the Common Grackle (Quiscula quiscula) by Howe (1976). Differential expenditure on the sexes at this stage might facilitate any sex differences in assimilation or competitive advantage later on. However, sex differences in assimilation efficiencies did not occur with Red Winged Blackbirds (Fiala and Congdon 1983).

Intra-sibling aggression may be very important in establishing sexual dimorphism. Up until the first 8-10 days the adults enter the nest to feed nestlings. Preferential feeding might explain the difference in size that occurs by this time. After this time, which corresponds to the period of fastest rate of growth, the nestlings have to crawl forward to the nest entrance and beg. In this scenario there is a great deal of opportunity for competition. Competition probably occurred as evidenced by the frequent outbursts of squalling which could be heard from within the nest. During the post-fledging period fighting was frequently seen between siblings and it seemed the females were the dominant sex. However, there was no evidence of females receiving more food than males after fledging.

C. Why does sexual dimorphism occur in Riflemen?

That female Riflemen necessarily need to be larger than males to be more effective in breeding is not testable. However, Riflemen show various characteristics suggesting that females are at or near the small limit of size for which they can breed successfully. These include (1) reversed from normal sexual dimorphism, (2) protracted breeding cycle (longer than that of any other NZ passerine), and (3) hole nesting habit and elaborate nest, which imply that maximising thermal insulation is very

important.

Sexual dimorphism is usually correlated with larger males and reduced male parental investment and polygamy (Ralls 1977). None of these correlates occurred with Riflemen. Instead males are smaller than females, males contribute significantly in parental care and Riflemen are monogamous. Where reversed sexual dimorphism has occurred in other bird taxa, differential niche use has been given as an explanation for the female's larger size (eg Yom-Tov and Ollason 1976). They suggested that larger bodied animals take larger and different food items. However, there was no evidence of a differential feeding niche occurring in Riflemen (see sections one and three).

In most monogamous birds, males are on the average slightly larger than females, and there is evidence that small sexual differences in mean body weight or in bill size are related to the problems of maintaining dominance relationships among pair members (Selander 1972). In Hummingbirds, as with Riflemen, a minimum female body size may be retained in order to produce a viable egg. However, Wolf (1969) found that the retention of sexual monomorphism was "in certain species rather the result of selection for similar aggressive signals when both males and females held feeding territories". There is likely to be more than one explanation applicable to different species for the degree of sexual dimorphism and for the direction of the size difference.

Rahn et. al. (1975) [in Yomtov and Ar (1982)] stated that the strain of producing eggs may be a factor influencing size dimorphism in the smaller species within an order, disregarding the breeding behaviour of the order, since single egg mass scales with body surface area rather than basal metabolic rate.

In this author's view sexual dimorphism in Riflemen (and the increased parental investment in female offspring) is necessary to enable females to

cope physiologically with the Rifleman's breeding demands (i.e. laying up to 100% of body weight with a clutch of five eggs). A possible advantage in producing larger females, then, is that a high relative investment in females facilitates increased fecundity because of the larger body size of females, while smaller parental effort can be invested in males because they are not required to lay eggs and can cope with the climate with a smaller body size. Hence a sex biased primary sex ratio does not occur because each sex of offspring has the same number of breeding opportunities and is of equal value in terms of future reproduction. In conclusion, differential parental investment for each sex is necessary to produce optimum reproductive value to parents in future generations to maximise fecundity while at the same time the average expected reproductive life span of male and female offspring is equal.

D. Comparisons with other Kowhai Bush passerines

It seems that Gill's calculated mean life expectancy of Grey Warbler must be an overestimate because it does not take into account the period which probably involves the highest risk: mortality in the first year of life. Even so, with using the method Riflemen seem to have a shorter life expectancy than Grey Warbler do. Further, the method yields an estimate of mortality which is within the range of 40-60% given for adult survival among small land passerines in temperate regions (Ricklefs 1972). A shorter life span might result in a greater time constraint for Riflemen to breed. Fewer breeding opportunities would probably place Riflemen under a different set of imperatives than Grey Warbler, like the need to develop larger females in order to maximise fecundity.

Powlesland (1983) found that the highest mortality of adult Robins occurred in the autumn and winter months and that (page 275) "a similar proportion of adult males and females died each season, except in winter

($P<0.05$), when a greater proportion of bachelors (unpaired adult males) (40% of 10) died than did adult paired males (13.3% of 60, $P < 0.05$). In contrast only 10.9% of 46 adult females died in winter." Thus the similar mortality found for each sex in this study has been observed in at least one other study of a Kowhai Bush passerine. This similarity in the degree of mortality and breeding life expectancy between the sexes is consistent with Fisher's (1958) theoretical prediction that the sexes must be of equal reproductive value to parents. Consequently there is no trade-off of differential parental investment in offspring of each sex with the expected survival of offspring in Riflemen.

E. Conclusions

Ricklefs (1968) (in Richter 1983) stated that the maximum growth rate of passerine birds occurs midway through the nestling period, and total energetic requirements may also peak before fledging (Hussell 1972, Ricklefs 1974). However, it is conceivable that parental investment in each sex after the nestling period may be significant in evaluating whether differential parental investment occurs. In order to make a comprehensive assessment of parental investment in the sexes, differential post-fledging parental investment needs to be considered. Preferential feeding during the post-fledging period was not apparent. However, female juveniles seemed to be better competitors than males for parental attention. It is concluded that Rifleman parents invest more in females to maximise fecundity. No adjustment in primary sex ratio occurs because they are probably rearing broods which are on average slightly smaller than the theoretical maximum possible.

SECTION FIVE : NESTBUILDING, TERRITORIALITY AND MOULT

A. INTRODUCTION

Three other activities occurred over the breeding cycle that involved an outlay of energy for parents. Nestbuilding and territorial behaviour may be regarded as a form of parental effort while moult involves an outlay of energy on the individual's behalf only. However, the relative onset of moult between parents may be influenced by any trade-off of parental effort on the current brood. If the male parent meets most of the demands of feeding the second brood then its moult might be delayed relative to the female parent.

The importance of nestbuilding is reflected in the complex structure of the first clutch nest and its design to maximise thermal insulation (section two). Although no measure of the total amount of time required to build a nest was possible, evidence of work partitioning was obtained during nest watches to determine how parents allotted time and energy to nestbuilding. It was hypothesised that parents would cooperate in nest building, with males undertaking most of the work.

Territorial defense could be considered a form of parental effort if this behaviour is interpreted as the defence of a food resource for offspring. It was hypothesised that the amount of territorial behaviour would be minimal and what territorial defense there was would be shared by the parents.

B. METHODS

1. Nestbuilding

Data on nestbuilding were obtained by observations. Visits with and without materials were recorded and the time spent in the nest building. Time spent in the nest was recorded with a stopwatch (one operated for each

parent). Each time nest-building was watched the weather conditions were subjectively scored as described in the General Methods section.

2. Territorial behaviour

Territorial behaviour was monitored by considering vocalisations, time spent in territorial behaviour during the courtship-feeding period, and observations of interactions with neighbours.

In order to determine if there was any sex role partitioning of territorial defense all the territorial disputes were documented and the following variables scored : (i) the number of disputes where both members of the pair were present and had the option to defend but only the male took the initiative and chased the intruding bird(s), (ii) as for (i) except where the female defended, (iii) only the male of the defending pair was present and defended and (iv) as for(iii) except where the female defended. Where the male and the female both attacked the "intruders" they were scored equally in variables (i) and (ii). This was only seen 3 times.

3. Moult

The presence or absence of moult was subjectively assessed from the appearance of the body feathers. The first sign of "patchiness" or missing primaries and tail feathers was taken to indicate that moult had started.

4. Vocalisations

Vocalisations were recorded on a Uher Report-L4000 reel to reel tape recorder using a Nakamichi CP4 microphone. Most recordings were made by following individuals while they foraged. Recordings of nestlings were made by siting the microphone near the nest entrance. The calls were

analysed on a Sonograph with the frequency range set from 160-16000 hz.

C. RESULTS AND DISCUSSION

1. Nestbuilding

A. Behavioural description

Nests were built at any time of the day and spasmodically over a few days. Either one bird would stay in the nest box presumably placing material while the other "passed in" material, or both birds would stay in the box nest for short intervals and progressively pull in material placed at the entrance.

B. Sampling conditions

Most nestbuilding was observed under similar and ideal weather conditions (Table 1).

Table 1 Weather conditions during observations of nestbuilding

Scale:	Wind	Temperature	Cloud
0	34	15	23
1	14	31	20
2	6	8	11
3	0	0	0
unrecorded	3	3	3

Twenty different first clutch nests were watched on 57 occasions : 25 times in 1980-81, 21 times in 1981-82 and 11 times in 1982-83. The average length of each observation period was 77.0 minutes (SD = 33.9) and the total time spent watching was 73.12 hours.

One second clutch nest was watched on 3 occasions for a total of 274 minutes. On one occasion weather conditions were not recorded. For one of the other two the wind, cloud and temperature were scored as 1, 1 and 0 respectively, and for the third sample these were scored 0, 3 and 0.

C. Comparison between parents of nestbuilding effort

(i) Visits with and without building material

Males made significantly more visits with and without material than females (Wilcoxon matched pairs sign rank tests $Z = 4.27$, $P < 0.001$; $Z = 2.23$, $P < 0.013$ respectively). The mean hourly rates of visits with building material for males and females were 8.6 (SD = 5.9, n = 56) and 4.4 (SD = 3.9, n = 57) respectively. Means and standard deviations for non-material visits were not calculated because there were too may zero values to make these calculations sensible. Males made on average 66% of the visits with building materials.

On the 3 occasions second clutch nestbuilding was watched, the average rate of building material visits for males and females were respectively 18.8 and 10.5 and non-material visits 1.2 and 2.0 per hour.

(ii) Time spent in the nest

Males did not spend significantly more time in the nests than females (Wilcoxon matched pairs sign rank test $Z = 1.43$, $P > 0.05$). The total time spent in the second clutch nest was 21.2 minutes for the male and 16.3 minutes for the female.

(iii) Conclusions

A similar pattern probably occurred in second clutch nest building as with the first clutch nests: Males did significantly more work than females in the construction of nests as reflected by their more frequent building visits. However, nestbuilding overall did not appear to require a lot of time in total as the proportion of time spent building over the pre-lay period was less than 1%.

The dominant role of the male in nest-building, the large numbers of partially built nests, and the behaviour of unpaired males in front of

females at nest boxes (Section three), suggests that male Riflemen initially chose sites which females finally accepted or rejected.

2. Territory and moult

A. Territory

Territorial behaviour of South Island Rifleman has been studied for 6 years by Gray (1974). Only the area of two territories were measured " one in Kanuka forest with a well developed hardwood understorey" and one in a pine (Pinus spp) plantation. Non-breeding territories were 1.6-2.0 ha while one was 0.8-1.2 ha within the breeding season. These compare with an average of 6.25 ha and 3.6 ha per pair in a North Island population in the Orongorongo Valley (Gaze pers comm). A later study in the same area revealed 3-4 pairs occupying 8 ha. In the pilot study population of this study 9-15 pairs bred successfully in 6 ha. Excluding the few pairs that might have gone unnoticed in the main study area, the number of pairs ranged from 15-17 in 80ha.

In Gray's Dunedin population, disputes over boundaries were most common in early spring and when fledglings had left the nest in early summer. No such pattern could be discerned from the Kowhai Bush populations. Over the time spent daily observing Riflemen (including continuous watching during the courtship-feeding period) in five breeding seasons from mid August to late January, only 63 territorial disputes were witnessed. Further, there was a large degree of overlap of territory boundaries and obvious disregard of each other's home range, as evidenced by frequent observations of pairs foraging around another's nest site.

The amount of time Riflemen spent in territorial behaviour during pre-lay and egglaying (courtship-feeding period) was less than one percent. By comparison over the prelay period, male and female Robins at Kowhai Bush spent 17% and less than 1% of their time respectively in vocalising and

territorial defence. While laying occurred males and females spent 6% and less than 1% respectively of their time in territorial behaviour. During the whole of the breeding season male Robins spent significantly more time in territorial defence than the females (Powlesland 1980).

The number of times males and females were involved in territorial interactions were not significanlty different (Table 2).

Table 2 Sex role partition in territorial defence

	Categories of defending territory holders					
	Total encounters involving M/F		Encounters where M or F had option		Encounters only one sex present	
Sex	M	F	M	F	M	F
Frequency of interactions	27	36	23	26	4	10
X^2	1.29, P > 0.05		0.08, P > 0.05		-	

The results of Chi square indicate no cause to reject the null hypothesis that there was no sex role partitioning of territorial defence between males and females.

B. Vocalisations

Riflemen do not have a song in the sense of a typical song bird singing from a song post advertising territory boundary. The Acanthisittadae have been noted for their simple syringeal musculature (Forbes 1882; Pycraft 1906; Ames 1971; reviewed in Sibley et. al. 1982). All of their calls were single notes or strings of single notes of similar high (around 7-13 Khz) frequency.

The vocalisation most often heard and which is commonly associated with Riflemen was an extremely short truncated single note "ssip" which was constantly exchanged between paired males and females while foraging together. A few of these single note calls were run together in a staccato fashion if a threat such as a Harrier Hawk (Circus approximans)

flew overhead. If a threat was more severe this low intensity alarm call preceded a "down trill" call. The down trill was the longest and most complicated call Riflemen made. It consisted of a series of extremely short notes run together and lasting a maximum of three seconds. The call started at a high frequency which dropped rapidly to a sustained note. Individual notes could often be discerned during the last phase of this call. Another call was apparently a modification of this alarm call and used to advertise position. It consisted of a series of similar notes further spaced apart than in the alarm call and without it s decrescendo characteristic.

When a pair became separated a two-note call was made comprising a strong short truncated note immediately followed by a slightly longer and lower frequency note that was also "cut short". This was the second most common note made by adult Riflemen. The last call made by adults was apparently a submissive call and rarely heard. It sounded the same as the juvenile begging call and consisted of a series of monotonic "sseep, sseep" calls whose length and frequency of repetition was graduated according to the degree of excitement. Adults gave these calls on the few occasions when birds were seen locked together fighting and by the female during copulation.

Juvenile calls consisted most frequently of the last call described above. However, juveniles could emit the adult repertoire before independance. Free-ranging juveniles were far more vocal than adults, and often contrived combinations of the contact call and single notes strung together similar to the adult's non-aggressive series. The last juvenile call was a begging call as described above which was similar to that given by older nestlings.

Because no time was spent in vocal advertisement of territory, and Riflemen vocalisations were simple in nature, it was concluded that vocal

behaviour was not an important consideration in assessing relative parental effort.

To assess the significance of work partition during nest-building and territorial behaviour it is necessary to gauge their importance relative to other energy outgoings during the breeding cycle. It appears from the amount of time spent in nestbuilding and territorial behaviour during the courtship-feeding period (less than 1%) that these activities do not constitute a relatively large outlay in energy. This conclusion is supported by the observations that a number of nests were often built before a site was selected (Gray 1974; this study), and that there were so few interactions observed between neighbouring birds.

The high male parental effort in nest-building and territorial behaviour are consistent with the prediction of the main hypothesis of this study. More investigation is required to ascertain whether this cooperativity during the breeding cycle extends into staggered moulting. It might be expected to do so given that moult starts for both parents before the breeding cycle has finished. Starting moult before the breeding cycle has finished is unusual for a small altricial land bird (Ricklefs 1974). There was some evidence of staggered moult with the females starting earlier, a pattern also observed in the Rock Wren (Xenicus gilviventris) (Heath pers comm) which is a confamilial of Riflemen.

C. Moult

From observations and the few moulting birds caught, it was determined that the annual adult moult involved the entire plumage. It was not possible from the few birds available to determine the sequence of moulting.

(i) Juveniles

Young Riflemen lost their juvenile plumage before the onset of winter. The speckled breast feathers were lost first, followed by the striated crown feathers on males. These were retained by females. It was not possible to determine whether this first moult involved any other feathers. After moulting had occurred juveniles were indistinguishable from adults.

(ii) Adults

Generally, moult started in the last 10 days of January often while second clutch nestlings were still being fed and observable moult (without the bird in the hand) lasted for about 50-60 days finishing by April. Hence moult was another demand on the energy resources of parents due to the energy required for feather formation and thermo-regulation (Lustik 1970). Given the male parent's dominant role in the care of second clutch offspring it was possible that peak energetic demands over this period might have been minimised by a delay in moult relative to the female's.

The moult of 14 pairs was followed by regular visual checks for outward appearances of moult to see if moult started earlier for one sex than the other. There were 6(43%) cases of the female starting moult before the male. With the other pairs it was not clear who started first. Without detailed moult schedules for males and females only the tentative conclusion may be drawn that females began moult before males.

The energetic cost of plumage replacement as a percentage of BMR (basal metabolic rate) is a function of body mass (Ricklefs 1974). Female Riflemen theoretically outlay 102% of BMR per day on moulting compared with 96% for males. As the moult is complete, the plumage weight replaced for females was theoretically 0.60g compared with 0.50g for males. Hence the

female replaced about 20% more plumage by weight than the male. Thus the apparently staggered moulting of Riflemen adults might be related to their sexual dimorphism in size and the concommittant requirement of the female for more time to complete moult before the need to gain condition for winter.

D. CONCLUSIONS

(1) Nesbuilding and territorial behaviour are not important energetic outgoings of parental effort relative to other forms of parental care.

(2) The high degree of parental cooperation, reflected in males undertaking most nestbuilding and about half of the territorial defence, was consistent with the main hypothesis of the thesis.

SECTION SIX: SYNTHESIS

A. Parental investment and sexual selection

1. Introduction

A small altricial passerine presents a good opportunity to investigate parental investment because (i) avian offspring display determinant growth and (ii) the reproductive cycle is energetically discrete because offspring become independant in the same breeding season they hatch.

In the Rifleman breeding system, male and female parental effort was directly comparable because it was qualitatively similar for both sexes throughout the breeding cycle. Territorial behaviour, which is usually the male's domain in passerines, was shared and was of little significance.

2. Relative parental investment and mate desertion

Even though the trend for the breeding cycle was one of higher male than female parental effort, it cannot be assumed that total male investment was higher than the female's. The factor hardest to account for in the balance of relative parental effort is the cost of producing eggs. Despite the male's large contribution during courtship-feeding the female still must undergo the stress of oogenesis. If an energy budget were available for females there would still be the difficulty of equating physiological stress (usually measured by cortisol levels) with energetic outlay. It is not possible, therefore, to falsify predictions from Triver's theory based on which sex invests most.

Trivers (1972) argued that the large initial investment in eggs puts the female at a disadvantage with respect to desertion. However, his argument also holds that (page 141) "if the net reproductive success for a male investing in the offspring of one female is larger than that gained from investing in the offspring of two females, then the male will be

selected to invest in the offspring of only one female". This study has shown that with Riflemen there is a high initial investment from the male in the first clutch in the form of courtship-feeding. Thus from the outset of the breeding season the risk of the male deserting the female must be minimal by Trivers's reasoning.

Dawkins and Carlisle (1976) criticised Trivers by arguing that the remaining future cost of raising young determines future behaviour. If residual cost is important, then the initially high investment by male Riflemen suggests that the remaining effort to rear offspring must approach equality with females. Hence there would be a sound basis for continued high male investment if Dawkins and Carlisle were correct. But the male's behaviour could be explained by consideration of other alternatives. In two seasons when Riflemen were studied, the chances of the male mating elsewhere were small as evidenced by the occurrence of unpaired male helpers and the virtual absence of unpaired female helpers.

Another explanation for the large amount of parental effort by Riflemen males relate to the consequences of leaving the female alone to feed young. On the one occasion that a male deserted or died, the female continued to feed the nestlings at a comparable rate to biparental feeding nests. Unfortunately this nest was preyed on and the effect of solo-parental care on nestling weights, nestling period and survival could not be determined. However, in another instance where the female deserted or died during the nestling period the nestlings fledged four days late, under the average fledging weight, and in obviously poor condition. Two nestlings were weak and unable to fly at all. It appeared that most of this brood died before the start of autumn.

Smith et. al. (1982) found with Song Sparrows (Melospiza melodia) that the young of unaided females grew more slowly, died more often and had less chance of surviving to independance than offspring from broods where

both parents fed. Although solo parents may be able to raise offspring unaided, evaluating the true cost of non-parental cooperation needs to include measuring the survival of individuals over consecutive seasons and comparing these results with individuals which cooperate.

The concept of future reproductive opportunities in the current season influencing later parental investment may be extended to include the remaining reproductive opportunities in later seasons (residual reproductive value sensu Pianka and Parker 1975). The idea that reproductive effort in the current season is a function of future survival is theoretically dependant on the animal's lifetime reproductive output being constant (Williams 1966). If the life expectancy of Riflemen is short and variable, then there would be a great deal of variability in reproductive life expectancy. Husbanding resources for future reproductive effort would not pay because of an individual's uncertain future. Rather, the observed high parental cooperation in a current brood seems the logical option.

3. Parental investment and sexual selection

The significance of courtship-feeding in Riflemen for sexual selection is that much of the male parent's initial investment occurs before copulation occurs.

With high male parental effort, mechanisms for preventing cuckoldry should occur in Riflemen. Cuckoldry during the courtship-feeding period was effectively prevented by the close contact maintained during foraging. In the course of courtship-feeding behaviour the male had the female continuously "under guard" with both sexes participating in what little intraspecific aggression occurred.

Helping behaviour only occurred after the nestling period had begun

and, therefore, after cuckoldry could have occurred. However, the timing of helper behaviour may have been a question of what suited the helper. Before chicks hatched it may have been more advantageous to spend time searching for unpaired adult females while there was still time enough to raise it s own brood.

Competition from other males for females could lead to high male investment during breeding. In monogamous species, a male's increased reproductive effort is disproportionate to the energy saved in reduced inter-male competition, which increases the males chances of surviving relative to the female (Trivers 1972). In Trivers's scenario it is conceivable that a preponderance of males might result but an increased number of males should be countered by a corresponding increase in inter-male competition as females become a limiting resource. There were more males than females at the start of three breeding seasons in the main study area, implying greater female than male mortality. However, the survival data (section four) do not support this conclusion. Although it is possible that inter-male competition has influenced male parental investment, it is this author's view that high male parental investment is instead born of necessity to ensure reproductive success.

4. Sexual dimorphism and parental investment

Sexual dimorphism in Riflemen may exist as a means of minimising intraspecific competition through niche separation. No differences between males and females in feeding niches were noticed during the courtship-feeding and post-fledging periods.

As there is no differential over winter survival of the sexes it seems there are no benefits from increased size to the female in its ability to tolerate the winter climate. Similar survival for the sexes supports the contention that the reason for the female's larger size is a functional

one, linked to the oogenesis of relatively large eggs. Apart from maximising the amount of resources available to the female that can be used for oogenesis, the retention of a larger body size could minimise the drop in thermo-regulatory efficiency encountered with being encumbered with such a relatively large non-thermogenic mass as the ova.

Data from this study present no case for rejecting Fisher's (1958) hypotheses relating differential parental investment, sex ratio and size sexual dimorphism. The main problem is ascertaining whether there is a corresponding differential parental investment (sensu Trivers) with rearing offspring which are sexually dimorphic in size. The possibility of the existence of differential maturation during the post-fledging stage needs to be established. The most thorough technique for this should incorporate energy budgets.

5. Parental investment and monogamy

Two advantages of a monogamous breeding system, particularly if Riflemen are energetically constrained, is year round fidelity and sedentariness (section three). Fidelity and sedentariness result in greater efficiency of early season reproduction because there is less time lost in pair bond establishment, or intrasexual competition. Also, boundaries of feeding ranges are probably well established and the greatest advantage can be made of "local knowledge".

Male parental care may also be a function of female manipulation as male ejaculate performance may be limited and this constraint serves as a means by which the female can control the male's attention (Dewsbury 1982). By delaying fertilisation as long as possible and/or requiring more than one copulation attempt for successful fertilisation, the female might foreclose options open to males to invest elsewhere. Dewsbury's theory is hard to falsify. In Riflemen, courtship-feeding started well before the

first copulation attempts were seen, which together with the protractedness of their breeding cycle might support the theory. However, the extent of courtship-feeding, its correlation with peak energy demands for egglaying, and the extent of male parental care support the hypothesis of this thesis that male parental care serves a functional role to offset the constraints of small size. Both factors, and others, may be acting in concert.

B. The chronology of the breeding cycle

The main features of the Rifleman breeding system which can be interpreted as minimising energetic constraints are the protracted length of laying, incubation and nestling periods. This protractedness has occurred without penalising the parents in other ways such as exposing the offspring to predation (except since the recent introductions of mammalian predators). Thus the protracted breeding cycle did not include a concommittant increase in the risk of predation whilst reducing the peak levels of energy required for parental care.

An alternative explanation for the protracted breeding cycles of endemic passerines has been offered by Gill (1980a). His thesis was that food availability in New Zealand is limited and does not allow the faster development that occurs in Northern Hemisphere temperate zone passerines. The northern hemisphere passerines introduced to New Zealand seem to have lengthened their breeding cycles or reduced their clutch sizes (Niethammer 1970). It is this author's view that the Rifleman's protracted breeding cycle reduces the peak energetic demands of breeding.

If energetic considerations influence parental behaviour then breeding behaviour should be correlated with climate, especially temperature. Finch's (1984) study on Abert's Towhee (Pipilo aberti) showed that 78% and 28% of the variation of the female's daily energy expenditure over the incubation and nestling periods respectively was explained by mean daily

air temperature. That air temperature was a significant influence on Rifleman behaviour was supported by the significant correlation of incubation behaviour with ambient temperature (section two).

Male cooperation in the Rifleman breeding system enabled the most efficient use of the time available. During incubation the females were afforded more time to forage and recover from egg-laying. The male's dominant role feeding first clutch young, especially fledglings, gave the female time to gain condition preparatory to laying second clutches. The male's principal role feeding second clutch young was possibly related to allowing females to prepare for and start moult earlier than males, as their moult demands were most likely higher than those of males.

C. Nonparental cooperation

The helping behaviour of unpaired adults supported the main hypothesis of this study. From the parents' point of view regular helping relieved them of some of the energetic burden of feeding young, which is the most costly form of parental care (Ricklefs 1974). The benefit to regular and casual helpers is apparently the acquisition of mates, which in view of the male Rifleman's short life span and uncertain breeding opportunities, justifies the cost (if any) in terms of fitness.

Helping by juveniles at their parent's second clutch nest, however, is unexplained although it could be a means of acquiring parental skills. Alternatively, their helping behaviour might be aimed at "buying" their presence in their parent's territory or increasing their inclusive fitness. However, it is possible that juvenile helping does not result in benefits towards themselves, the offspring or their parents. Instead their behaviour might be a stereo-typed response to begging calls and other birds feeding offspring.

D. Conclusion

The achieved objective of this study has been to demonstrate a high degree of parental cooperation among Riflemen which was predicted by the main hypothesis that Riflemen are constrained by their small size.

SUMMARY

1. COURTSHIP-FEEDING

Male Riflemen courtship-fed their mates from about two weeks before egg-laying until incubation started. Riflemen eggs were about 19% of the female body weight and were laid every 48 hours. It was estimated that females gathered enough food for maintenance and courtship-feeding supplied the deficit required for oogenesis. The 48 hour laying cycle also reduced the energetic burden of laying females.

Pairs of Riflemen kept in constant contact with each other during courtship-feeding which increased the efficiency of males feeding females. The conspicuous lack of ceremony and the males' habit of approaching the female with food removed the possibility of courtship-feeding detracting from the females' foraging efficiency.

2. INCUBATION

The length of the incubation period was about 20 days which is exceptionally long for a passerine. Male parents spent about half as much time again incubating as did the females, thus leaving females with about two hours a day more than males for foraging. The reduction in male attentiveness during the early stage of the second clutch incubation period was less than at other times of the breeding cycle which probably reflected a compromise between other energetically more expensive concurrent demands of feeding first clutch offspring.

During the night females incubated alone which was interpreted as being consistent with females conserving energy while recuperating from egglaying.

3. NESTLING PERIODS

The Rifleman nestling period was about 24 days long which is exceptionally long for a small passerine. Brooding lasted for 12 days and was equally shared by the parents. The most energetically demanding task of feeding young was performed mainly by the male who made about 66% of the feeding visits. Food delivered by parents was qualitatively similar within any nest category but parents of nests where helpers occurred fed larger items than parents of nests without helpers.

Two types of helpers were identified - regulars and casuals. Regulars contributed food at only one nest for the last 2/3 of the nestling period while casuals helped at more than one nest and to a varying degree. Helpers were mainly unpaired adult males or juveniles from the current year's offspring and continued to help feed fledglings. It was hypothesised that the reason adult males helped was to gain a mate, as some helpers were seen pairing with females from the brood which they had been helping.

Both parents at nests which were helped fed less than parents at nests without helpers, but male parents benefited most from the presence of helpers. Fledglings from helped nests did not weigh significantly more than those from other nests.

During the night the females brooded alone while males perched outside near the nest.

4. POST-FLEDGLING PERIOD

Male parents fed fledglings of both broods about half as much again as females. While feeding the first brood this result was interpreted as reflecting the female husbanding resources for second clutch laying. The males' behaviour feeding second broods could have allowed females to start moult sooner as moulting was theoretically more energetically expensive for

females.

Parents of broods with attendant regular helpers fed less than parents of non-helped broods with male parents benefiting most.

5. SEXUAL DIMORPHISM, SEX RATIO AND PARENTAL INVESTMENT

The primary sex ratios of first and second clutch broods from both study areas were unity. Female nestlings weighed significantly more than males from seven days onward. Even though averages of other female dimensions were larger than males during the nestling period they were not consistently significantly different. Males attained adult weight one day earlier than females but otherwise there was no indication of differential maturation.

Females from unisex broods were significantly lighter than females from mixed sex broods as expected if females are more costly to rear than males. It was concluded that females required more parental effort to raise and that this differential is met without primary sex ratio adjustment because Riflemen are probably rearing broods smaller than the maximum theoretically possible.

The survival of male and female offspring and male and female adults was equivalent. Using average adult mortality figures the average life-span of males and females was 1.7 and 2.2 years respectively. Immigration and emigration out of and into the two study areas was minimal.

6. NESTBUILDING, TERRITORIALITY AND MOULT

Males undertook 2/3 of the building of first clutch nests and probably did most of the second clutch nest building as well. Parental effort in territorial defense was equally shared although there was little time spent in territorial behaviour of any kind. There was some evidence to suggest that females moulted before males which might explain why males undertake

most of the parental care of second clutch young.

7. CONCLUSION

The results of this study confirm the main hypothesis tested : that Riflemen employ a highly cooperative parental care system which was predicted by the thesis that Riflemen are energetically constrained because of their small size.

THESIS BIBLIOGRAPHY

ALATALO, RV; GUSTAFSSON, LARS and LUNDBERG, A (1984) "High frequency of cuckoldry in Pied and Collared Flycatchers" Oikos 42:41-47

ASKENMO, C (1979) "Reproductive effort and return rate of male Pied Flycatchers" American Naturalist 114:748-752

BAILEY, RE (1952) "The incubation patch of passerine birds" Condor 54:121-136

BAILEY, CG and RIEGERT, PW (1972) "Energy dynamics of Encoptolophus sordidus costalis (Scudder) (Orthoptera:Acrididae) in a grassland ecosystem" Canadian Journal of Zoology 51:91-100

BIEBACH, H (1979) "Energetik des brutens biem star (Sturnus vulgaris) Journal fur Ornithologie 120:121-138

BIERMANN, GC and ROBERTSON, RJ (1981) "An increase in parental investment during the breeding system" Animal Behaviour 29:487-489

BIRKHEAD, ME (1981) "The social behaviour of the Dunnock Prunella modularis " Ibis 123(1):75-84

BLACK, CP (1975) "The ecology and bioenergetics of the northern black throated blue warbler (Dendroica caerulescens caerulescens)" Unpub. PhD. Dissert. Hanover, NH, Dartmouth College.

BRODY,S (1964) "Bioenergetics and gowth with special reference to the efficiency complex in domestic animals" Hafner Publishing Company Inc. New York

BROWN, JL (1970) "Cooperative breeding and altruistic behaviour in the Mexican Jay, Aphelocoma ultramarina " Animal Behaviour 18:366-378

BROWN, JL (1978) "Avian communal breeding systems" Annual Review of Ecological Systematics 9:123-155

BURSELL, E and TAYLOR, P (1980) "An energy budget for Glossina (Diptera:Glossinidae" Bulletin of Entomological Research 70:187-196

CALDER, WA (1974) "Consequences of body size for avian energetics" in Paynter, RA (ed) "Avian energetics" Publication of the Nuttal Ornithological Club Number 15:86-144

CASE, TJ (1978) "Endothermy and parental care in the terrestrial vertebrates" American Naturalist 112(987):861-874

COMAR,CL and DRIGGERS,JC (1949) "Secretion of radioactive calcium in the Hen's egg" Science 109:282

CUMMINS, KW and WUYCHECK, JC (1971) "Caloric equivalents for investigations in ecological energetics" Mitt. Verein. Limnol. No.18

CUNNINGHAM, JB (1984) "Differentiating the sexes of the Brown Creeper" Notornis 31(1):19-23

DAWKINS, R and CARLISLE, TR (1976) "Parental investment and mate desertion a fallacy" Nature (London) 262:131-133

DEWSBURY, DA (1982) "Ejaculate cost and male choice" American Naturalist 119(5):601-610

DRENT, RH (1972) "Adaptive aspects of the physiology of incubation" Proceedings of the International Ornithological Congress 15:231-256

DRENT, RH (1975) "Incubation" in Farner,DS and King, JR "Avian biology volume V" Academic Press NY

DRENT, RH and DAAN, S (1980) "The prudent parent:energetic adjustments in avian breeding" Ardea 68:225-252

EL WAILLY, A (1966) "Energy requirements for egglaying and incubation in the Zebra Finch, Taeniopygia castanotis " Condor 68:582-594

EMLEN, ST (1978) "The evolution of cooperative breeding in birds" in KREBS, JR and DAVIES, NB (eds) "Behavioural ecology: an evolutionary approach" Sinauer Assoc. Inc. Sunderland Mass. USA

FARNER, DS (1955) "Bird banding in the study of population dynamics" pp 397-449 in Wolfson, A (ed) "Recent studies in avian biology" University of Illinois Press, Urbana

FIALA, K (1981) "Reproductive cost and the sex ratio in Red Winged Blackbirds" pp198-213 in RD Alexander and DW Tinkle (eds) "Natural selection and social behaviour" Chiron Press

FIALA, K and CONGDON, JD (1983) "Energetic consequences of sexual size dimorphism in nestling Red Winged Blackbirds" Ecology 64(4): 642-647

FINCH, DM (1984) "Parental expenditure of time and energy in the Abert's Towhee (Pipilo aberti)" Auk 101(3):473-487

FISHER, RA (1958) "The genetical theory of natural selection" Clarendon Press, Oxford

FLACK, JAD (1979) "Biology and ecology of the South Island Robin" in HUNT, DM and GILL, BJ (eds) "Ecology of Kowhai Bush, Kaikoura" Mauri Ora Special Publication 2:22-27

FLEMING, CA (1979) "The geological history of New Zealand and its life" Auckland University Press

GIBB, JA (1954) "Feeding ecology of tits with notes on Treecreeper and Goldcrest" Ibis 96:513-543

GIBB, J (1957) "Food requirements and other observations on captive tits" Bird Study 4:207-215

GIBB, J (1961) "Biology and comparative physiology of birds" Volume 2 Academic Press, New York

GILBERT, AB (1971) "The female reproductive effort" pp1153-1162 In: Bell, DJ and Freeman, BM (eds) "Physiology and biochemistry of the domestic fowl" Volume 3, Chapter 49. Academic Press London.

GILL, BJ (1980) "Breeding of the Grey Warbler with special reference to brood-parasitism by the Shining Cuckoo" Unpub. PhD Thesis, University of Canterbury, Christchurch, NZ pp179

GILL, BJ (1980) "Abundance, feeding and morphology of passerine birds at Kowhai Bush, Kaikoura, New Zealand" New Zealand Journal of Zoology 7:235-246

GILL, BJ; POWLESLAND, RG and POWLESLAND, MH (1983) "Laying seasons of three insectivorous song-birds at Kowhai Bush Kaikoura" Notornis 30:81-85

GRAU, CR (1976) "Ring structure of avian egg yolk" Poultry Science 55:1418-1422

GRAY, RS (1969) "Breeding biology of Rifleman at Dunedin" Notornis 16:5-19

GRAY, RS (1974) "The territoriality of the South Island Rifleman near Dunedin" Post Graduate Diploma of Science in Zoology Thesis, University of Otago New Zealand

GURR, L (1947) "Measuring bird dimensions" Notornis 2 (4): 87-97

HAILS, CJ and BRYANT, DM (1979) "Reproductive energetics of a free living bird" Journal of Animal Ecology 48:471-482

HIRSHFIELD, ME and TINKLE, DW (1975) "Natural selection and the evolution of reproductive effort" Proceedings of the National Academy of Science USA 72:2227-2231

HOPSON, JA (1973) "Endothermy, small size and the origin of mammalian reproduction" American Naturalist 107:446-451

HOWE, HF(1977) "Sex-ratio adjustment in the common grackle" Science 198:744-46

HOWE, HF (1978) "Initial investment, clutch size and brood reduction in the common grackle" Ecology 59(6):1109-1122

HURNARD, SM (1978) "Climatic factors in the seasonality of New Zealand insects a meteorological viewpoint" New Zealand Entomologist 6(4):337-343

HUSSELL, DT (1972) "Factors affecting clutch-size in Arctic passerines" Ecological Monographs 42:317-364

JONES, PJ and WARD, P (1976) "The level of reserve protein as the proximate factor controlling the timing of breeding and clutch size in the red billed quelea Quelea quelea " Ibis 118:547-574

KENDEIGH, SC (1941) "Length of day and energy requirements for gonad development and egg-laying in birds" Ecology 22:237-248

KENDEIGH, SC (1952) "Parental care and evolution in birds" Illinois Biological Monographs 22:1-356

KENDEIGH, SC (1963) "Thermodynamics of incubation in the House Wren, Troglodytes troglodytes " Proceedings of the 13th International Ornithological Congress (Ithaca) pp884-904

KENDEIGH, SC; KRAMER, TC and HAMERSTROM, F (1956) "Variations in egg characteristics of the House Wren" Auk 73: 42-65

KENDEIGH, SC (1973) "Discussion on incubation" in "Breeding biology of birds" DS Farner (ed) pp78-107 National Academy of Sciences, Washington DC

KENDEIGH, SC; DOL'NIK, VR and GAVRILOV, VM (1977) "Avian energetics" in Pinowski, J and Kendeigh, SC (eds) "Granivorous birds in ecosystems" Cambridge University Press, Cambridge pp127-204

KING, JR (1972) "Energetics of reproduction in birds" In: Farner, DS (ed) "Breeding biology of birds" Proceedings of a symposium on breeding behaviour and reproductive physiology in birds. National Academy of Sciences, Washington DC.

KLOMP, H (1970) "The determination of clutch size in birds: a review" Ardea 58: 1-124

KREBS, JR (1970) "The efficiency of courtship-feeding in the Blue Tit Parus caerulus " Ibis 112:108-110

LACK, D (1968) "Ecological adaptations for breeding in birds" Methuen London.

LANDSBOROUGH-THOMSON, A (1964) "A new dictionary of birds" Nelson Pub. London, Edinburgh pp928

LIGON, JD (1983) "Cooperation and reciprocity in avian social systems" American Naturalist 121(3):366-384

LUSTICK, S (1970) "Energy requirements of moult in Cowbirds" Auk 87:742-746

MC LEAN, IG (1980) "The influence of song behaviour and breeding success on spacing between nests of the Fantail Rhipidura fuliginosa " Ibis 122:98-102

MURTON , RK and WESTWOOD, NJ (1977) "Avian breeding cycles" Clarendon Press Oxford

MERTENS, JAL (1980) "The energy requirements for incubation in Great Tits, Parus parus L." Ardea 65:184-196

MOEED, A and FITZGERALD, BM (1982) "Foods of insectivorous birds in forest of the Orongorongo Valley, Wellington, New Zealand" New Zealand Journal of Zoology 9:391-403

MUGAAS, JN (1976) "Thermal energy exchange, mocroclimate analysis, and begavioural energetics of Black-billed Magpies, Pica pica hudsonii " Unpub. PhD. Diss. Pullman Washington State University

NEEDHAM, J (1963) "Chemical embryology" Volume 1. Hafner Publishing Company New York and London

NIETHAMMER, G (1970) "Clutch sizes of introduced European passeriformes in New Zealand" Notornis 17:214-222

NISBET, ICT (1983) "Courtship-feeding, egg size and breeding success in Common Terns" Nature, London 241:141-142

NORRIS, RA (1958) "Comparative biosystematics and life history of the Nuthatches Sitta pygmaea and Sitta pusilla " University of California Publications in Zoology 56:119-300

NUR,N (1984) "Consequences of brood size for breeding Blue Tits 2.Nestling weight, offspring survival and optimal brood size" Journal of Animal Ecology 53(2): 497-519

PERRINS, CM (1969) "The timing of bird's breeding seasons" Ibis 112:242-255

PETRUSEWICZ, K and MACFADYEN, A (1970) "Productivity of terrestial animals. Principles and methods" IBP Handbook No.13. Blackwell Scientific Publications. Oxford and Edinburgh

PIANKA, ER and PARKER, WS (1975) "Age specific reproductive tactics" American Naturalist 109:453-464

POWLESLAND, MH (1982) "A breeding study of the South Island Fantail (Rhipidura fuliginosa fuliginosa)" Notornis 29:181-195

POWLESLAND, RG (1979) "Time budgets of the South Island Robin" in Hunt, DM and Gill, BJ (eds) "Ecology of Kowhai Bush, Kaikoura" Mauri Ora Special Publication #2: 28-31

POWLESLAND, RG (1981) "A time budget study of the South Island Robin (Petroica australis)" Unpublished Ph D dissertation, University of Canterbury, New Zealand pp700

POWLESLAND, RG (1983) "Breeding and mortality of the South Island Robin in Kowhai Bush, Kaikoura" Notornis 30(4): 265-283

PUGESEK, BH (1983) "The relationship between parental age and reproductive effort in the California Gull (Larus californicus)" Behavioural Ecology and Sociology 13: 161-171

RAHN, H and AR, A (1974) "The avian egg: incubation time and water loss" Condor 76:147-152

RALLS, K (1977) "Sexual dimorphism in mammals: Avian models and unanswered questions" American Naturalist 111(981):917-938

RICHTER, W (1983) "Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics" American Naturalist 121(2): 158-171

RICKLEFS, RE (1967) "A graphical method of fitting equations to growth curves" Ecology 48:978-983

RICKLEFS, RE (1968) "Patterns of growth in birds" Ibis 110:419-451

RICKLEFS, RE (1969) "Preliminary models for growth rates of altricial birds" Ecology 58: 31-45

RICKLEFS, RE (1972) "Fecundity, mortality and avian demography" in "Breeding biology of birds - Proceedings of a symposium on breeding behaviour and reproductive physiology in birds" National Academy of Sciences Washington DC

RICKLEFS, RE (1974) "The energetics of reproduction in birds" in Paynter, RA Jnr (ed) "Avian energetics" Nuttal Ornithological Club Number 15:152-297

RICKLEFS, RE (1977) "On the evolution of reproductive strategies in birds: reproductive effort" American Naturalist 111:453-478

ROBERTSON, HA and DENNISON, MD (1984) "Sexual dimorphism of the Chatham Island Warbler Gerygone albofronta " Emu 84(2): 103-108

ROBERTSON, HA; WHITAKER, AH and FITZGERALD, BM (1983) "Morphometrics of forest birds in the Orongorongo Valley, Wellington, New Zealand" New Zealand Journal of Zoology 10(1): 87-97

ROBERTSON, RJ and BIERMANN, GC (1979) "Parental investment strategies determined by expected benefits" Zietschrift fur Tierpsychologie 50: 124-128

ROYAMA, T (1966a)"A reinterpretation of courtship-feeding" Bird Study 13(2): 116-129

ROYAMA, T (1966) "Factors governing feeding rate, food requirement and brood size of nestling Great Tits (Parus major)" Ibis 108(3): 313-348

SCHAFFER, WM (1974) "Selection for optimal life histories: The effects of age structure" Ecology 55: 291-303

SCOTT, DM and ANKNEY, CD (1979) "Evaluation of a method for estimating the laying rate of Brown Headed Cowbirds" Auk 96: 483-488

SELANDER, RK (1972) "Sexual selection and dimorphism in birds" in Chapter 8 B Campbell (ed) "Sexual selection and the descent of man" London Heinemann

SIBLEY, CG; WILLIAMS, GR and AHLQUIST, JE (1982) "The relationships of the New Zealand wrens (Acanthisittadae) as indicated by DNA-DNA hybridisation" Notornis 29(2): 113-130

SIEGEL, S (1956) "Nonparametric statistics for the behavioural sciences" International Student Edition 312pp McGraw-Hill International Book Company, Japan.

SKUTCH, AF (1957) "Incubation patterns of birds" Ibis 99: 69-93

SLOBODKIN, LB and RICHMAN, S (1961) "Calories/gram in species of animals" Nature, London 191: 299

SMITH, JNM (1978) "Division of labour by song sparrows feeding fledged young" Canadian Journal of Zoology 56(2): 187-191

SMITH, JNM; YOM-TOV, Y and MOSES, R (1982) "Polygyny, male parental care and sex ratio in song sparrows: and experimental study" Auk 99: 555-564

SNEDECOR, GW and COCHRAN, WG (1980) "Statistical methods" Iowa State University Press USA pp507

SOKAL, RR and ROHLF, FJ (1981) "Biometry" second edition, WH Freeman and company, San Francisco, p859

SOPER, MF (1976) "New Zealand birds" Second edition. Whitcombe and Toombs Pub Wellington, New Zealand

STALLCUP, JA and WOOLFENDEN, GE (1978) "Family status and contributions to breeding by Florida Scrub Jays" Animal Behaviour 26(4): 1144-1156

STEAD, EF (1932) "Life histories of New Zealand birds" London Search Publishing 161pp

TASKER, CR and MILLS, JA (1981) "A functional analysis of courtship-feeding in the Red-Billed Gull, Larus novaehollandiae scopulinus " Behaviour 77: 222-241

THOMAS, BT (1979) "Behaviour and breeding of the white bearded flycatcher (Canopias inornata)" Auk 96:767-775

TRIVERS, RL (1971) "The evolution of reciprocal altruism" Quarterly Review of Biology 46:35-57

TRIVERS, RL (1972) "Parental investment and sexual selection" in Campbell, B (ed) "Sexual selection and the descent of man" Chicago Aldine

TRIVERS, RL and WILLARD, DE (1973) "Natural selection of parental ability to vary the sex ratio of offspring" Science 179:90-92

TUOMI, J; HAKALA, T and HAUKIOJA, E (1983) "Alternative conepts in reproductive effort, costs of reproduction and selection in life history evolution" American Zoologist 23(1): 25-35

VERNER, J (1965) "Time budget of the male Long Billed Marsh Wren during the breeding season" Condor 67: 125-139

VERNER,J and WILLSON, M (1969) "Mating systems, sexual dimorphism and the role of male North American passerine birds in the nesting cycle" Ornithological Monographs 9: 1-76

VINCE, MA (1969) "Embryonic communication, respiration and the synchronisation of hatching" in Hinde, RA (ed) "Bird vocalisations" Cambridge University Press

VLECK, CM (1981) "Energetic cost of incubation in the Zebra Finch Poephila guttata " Condor 83(3): 229-237

WALKER, HM and LEV, J (1969) "Elementary statistical methods" Third Edition, 432pp, Holt, Rinehart and Winston, Inc., USA.

WALSBERG, GE (1977) "Ecology and energetics of contrasting social systems in Phainopepla nitens (Aves:Ptilogonatidae)" University of California Publications in Zoology 51:92-103

WALSBERG, GE (1983) "Avian ecological energetics" in Farner, DS; King, JR and Parkes, "Avian biology" Volume 7

WALSBERG, GE and KING, JR (1978a) "The heat budget of incubating Mountain White-crowned Sparrows (Zonotrichia leucophrys oriantha) in Oregon" Physiological Zoology 51:92-103

WALSBERG, GE and KING, JR (1978b) "The energetic consequences of incubation for two passerine species" Auk 95:644-655

WELTY, JC (1975) "The life of birds" Second Edition. Saunders, Philadelphia.

WHITE, FN and KINNEY, JL (1974) "Avian incubation" Science 186:107-115

WILLIAMS, GC (1966) "Natural selection, the costs of reproduction, and a refinement of Lack's Principle" American Naturalist 100(916): 687-690

WILLIAMS, GR (1973) "The natural history of New Zealand an ecological study" pp434 AH and AW Reed Ltd Publishers

WOLF, LL (1969) "Female territoriality in a tropical Hummingbird" Auk 86: 490-504

WOOD-GUSH, DGM and HORNE, AR (1970) "The effect of egg formation and laying on the food and water intake of Brown Leghorn Hens" British Poultry Science 11: 459-466

WOOLFENDEN, GE (1975) "Florida Scrub Jays at the nest" Auk 92: 1-15

YOM-TOV, Y and AR, A (1982) "Criticism of Vonschantz and Nilsson's hypothesis on the reasons for the reversed size dimorphism in birds of prey" Oikos 38(3): 387-388

YOM-TOV, Y and OLLASON, JG (1976) " Sexual dimorphism and sex ratios in wild birds" Oikos 27: 81-85

ZAHAVI, A (1974) "Communal nesting of the Arabian Babbler. A case of individual selection" Ibis 116: 84-87

APPENDIX 1 : References used to calculate calorific equivalents of invertebrates in the rifleman diet

COLEOPTERA:
CAMPBELL, A AND DINHA, R.N (1978) "Bioenergetics of granivorous beetles, Cryptolestes ferrugineus and Rhyzopertha dominica (Coleoptera: Cucujidae and Bostrichidae)" Can. J. Zool.56: 624-633

HAGVAR,S (1975) "Energy budget and growth during the development of Melasoma collaris (Coleoptera)" Oikos 26: 140-146

KLEKOWSKI,R.N.;PRUS,T; ZYROMSKA-RUDZKA,H (1967) "Elements of energy budget of Tribolium casteneum (Hbst) in its developmental cycle " in K. Petrusewicz (Ed) "Secondary Productivity of Terrestial Ecosystems #2 :859-879. Warszawa-Krakow, PWN.

PRUS,T (1970) "Calorific value of animals as an element of bioenergetical investigations" Pol. Arch. Hydrobiol. 17(30)1/2:183-199

RANDOLPH, J.C.; RANDOLPH, P.C. and BARLOW, C.A. "Variations in energy content of some carabid beetles in eastern Canada" Can.J.Zool.54:10-18

WIGHTMANM J.A. (1978) "The ecology of Callosobruchus analis (Coleoptera: Bruchidae): Energetics and energy reserves of the adults" Journal of Animal Ecology 47:131-142

SPIDERS:
NORBERG,R.AKE (1978) "Energy content of some spiders and incects on branches of Spruce (Picea abies) in winter; prey of certain passerine birds" Oikos 31:222-229

LEPIDOPTERA:
SCHROEDER, L.A.(1976) "Energy, matter and nitrogen utilization by the larvae of the Monarch Butterfly Danaus Plexippus " Oikos 27:259-264

SCHROEDER, L.A.(1977) "Calorific equivalents of some plant and animal material - the importance of acid corrections and comparison of precision between the Gentry Wiegert Micro and the Parr Semi-Micro bomb calorimeters" Oecologia (Berl) 28:261-267

MACKEY, A.(1978) "Growth and bioenergetics of the moth Cyclophragma leucosticta Grunberg" Oecologia 32:367-376

ORTHOPTERA:
CAREFOOT, T.H.(1977) "Energy partitioning in the desert locust, Schistocerca gregaria (Forsk.)" Acrida 6:85-107

GOLLEY,F.B.(1961) "Energy values of ecological materials" Ecology 42:581-584

WHITE,E.G.(1978) "Energetics and consumption rates of alpine grasshoppers (Orthoptera: Acrididae) in New Zealand" Oecologia 33:17-44

WIEGART,R.G.(1967) "Investigation of secondary productivity in grasslands" pp.499-518 in "Proceedings of a working meeting on the principles and methods of secondary productivity of terrestial ecosystems" Warsaw 1966

DIPTERA:
BURSELL,E. and TAYLOR,P. (1980) "An energy budget for *Glossina* (Diptera: Glossinidae)" Bull.Ent.Res.70:187-196

HOFSVANG, TROND (1973) "Energy flow in *Tipula excisa* Schum. (Diptera,Tipulidae) in a high mountain area, Finse, South Norway" Norw.J.Zool.21:7-16

GENERAL:
BAILEY, CG and RIEGERT, PW (1972) "Energy dynamics of *Encoptolophus sordidus costalis* (Scudder) (Orthoptera: Acrididae) in a grassland ecosystem" Can. J. Zool. 51:91-100

CUMMINS, KW and WUYCHECK, JC (1971) "Caloric equivalents for investigations in ecological energetics" Mitt. Internat. Verein. Limnol. No.18

SLOBODKIN, LB (1962) "Energy in animal ecology" In Cragg, JB (ed) "Advances in ecological research" Volume 1:69-101. London Academic Press.

SLOBODKIN, LB and RICHMAN, S (1961) "Calories per gram in species of animals" Nature, London 191:299

APPENDIX 2 : Breeding characteristics of five Kowhai Bush passerines

CHARACTERISTIC	ROBIN	GREY WARBLER	RIFLEMAN	BROWN CREEPER	FANTAIL
X CLUTCH SIZE	2.7	3.97	4.4	3.7	3.5
SD	0.5	0.28	0.5	0.5	0.5
n	100	39	106	22	142
Broods-1,2/2+	2+	2	2	2	2+
Female : Egg weight weight	13%	23%	22%	18%	19%*
Egg weight X	?	1.5	1.34	?	?
SD		0.08	0.40		
N		9	40		
Female : Clutch weight weight	35%	91%	85%	67%	66%
Laying Interval	24 Hrs	48 Hrs	48 Hrs	24 Hrs	24 Hrs
X start of lay	15.8	8.9,12.9	22.9	1-7.10	1-2.10
Years Observ	78,79	76,77	80,81,82	80,81	77
Incubtn Behav.	Female	Female	Fem+Mal	Female	Fem+Mal
Courtship Feed in prelay+lay	both	neither	both	both	Prelay lay=?
Courtship Feed in incubation	yes	no	no	yes	no
Nestling Period	20.8	17.2	24.0	20.0	12.6
SD	?	0.9	1.2	0.6	0.7
N	19	52	50	41	11
Incubation Pd	17.7	19.5	19.7	19.2	14.2
SD	?	1.2	0.8	1.1	0.6
N	30	14	80	38	34

Adult weights (X,SD,N)	Male	Female
Robin	34.9,1.3,27	35.1,2.6,18
Greywarbler	6.4,0.4,50	-
Rifleman	5.6,0.3,33	7.0,0.7,20
Brown Creeper	13.4,0.7,51	11.0,0.4,24
Fantail	7.9,0.7,17	-

Authorities Robins - R.G.Powlesland pers.comm., Powlesland (1982)
Grey Warbler - B.J.Gill pers.comm., Gill (1983) Brown Creepers - J.B.Cunningham pers.comm.
Fantails - M. Powlesland, Powlesland (1982), Gill (1980)
* = egg weight deduced from egg dimensions

from Powlesland (1982) and the relationship wt =klB2, k was taken as the same as that for Grey Warblers after Gill (1983).

Notes : (i) nestling period - day of hatching is counted as day one, day of fledging is counted as the nth day
(ii) incubation period = number of days elapsed from the last day of laying until the day of hatching (all the above species clutches hatch within 24 hours)
(iii) adult weight - Greywarbler and Fantail are sexually monomorphic. Greywarbler and Fantail weights measured in winter.18.2

APPENDIX 3: Number of nests in both study areas that started laying, hatched and fledged young for each calendar week

Month:	September				October				November				December				January			
Week :	1	2	3	4:1	2	3	4:1	2	3	4:1	2	3	4:1	2	3	4				
Laying:	1	15	27	25:2	2		1:4	4	8	6:1	1		:							
Hatching:				:6	25	22	24:3	1	2	1:3	7	6	5:1							
Fledging:				:			10:22	22	18	6:	2	4	5:8	9	5	3				

Notes:(1) week 1 = days 1 - 7, week 2 = days 8 - 15, week 3 = days 16 - 22, week 4 = days 23 - 30/31 of a given month.
(2) where only the start or stop date of one phase of the breeding cycle was known the other dates were determined by extrapolation using mean times for the remaining phases.
(3) nests that were preyed on were used (by extrapolation as above) if the starting date of at least one phase of their breeding cycle was known.
(4) second clutch data from the 1983/84 season were not used because these nests were not regularly checked.
(5) these data do not include "relay" nests

APPENDIX 4: Weather recordings from various meteorological stations kept in Kowhai Bush, Kaikoura

A. Temperature (°C)

Notes : (i) Monthly averages were calculated by summing the daily maximum and minimum temperatures and dividing these by two to yield the daily mean. Daily means were used to calculate the monthly means in the usual manner.

(ii) Monthly mean maxima and minima were calculated by using the highest and lowest temperatures recorded in a 24 hour period and then calculating the monthly means in the usual manner.

(iv) Overall averages were calculated by summing all the monthly averages and dividing by the number of years monthly averages were calculated.

(v) Data from 1977 and 1978 were taken from a weather station outside of the bush (station number G23351) and data from 1981,82 and 83 were from taken from a station situated about 40m into the bush at the SchoolHouse Road end.

Temperature year	month	mean min X	SD	N	mean max X	SD	N	month mean	rain fall(mm)
1977	Jan	–	–	–	–	–	–	–	–
	F	–	–	–	–	–	–	–	–
	M	–	–	–	–	–	–	–	–
	A	–	–	–	–	–	–	13.1	40.3
	M	–	–	–	–	–	–	8.7	106.7
	J	–	–	–	–	–	–	7.6	99.6
	J	–	–	–	–	–	–	7.1	279.1
	A	–	–	–	–	–	–	7.6	188.7
	S	–	–	–	–	–	–	6.8	146.0
	O	–	–	–	–	–	–	10.1	71.5
	N	–	–	–	–	–	–	11.4	80.5
	D	–	–	–	–	–	–	13.4	33.5
1978	Jan	–	–	–	–	–	–	17.1	32.0
	F	–	–	–	–	–	–	16.8	73.0
	M	–	–	–	–	–	–	15.5	80.5
	A	–	–	–	–	–	–	14.1	68.0
	M	–	–	–	–	–	–	10.2	157.9
	J	–	–	–	–	–	–	6.7	323.0
	J	–	–	–	–	–	–	8.1	295.5
	A	–	–	–	–	–	–	9.0	103.0
	S	–	–	–	–	–	–	–	174.5
	O	–	–	–	–	–	–	10.5	84.0
	N	–	–	–	–	–	–	13.3	45.5
	D	–	–	–	–	–	–	14.6	60.9
1981	Aug	4.9	2.3	15	13.0	5.7	15	9.0	
	S	3.1	1.8	27	15.7	3.0	26	9.4	
	O	5.1	2.0	24	16.6	4.4	24	10.8	
	N	8.4	3.0	29	17.4	3.3	30	12.9	
	D	11.4	2.9	31	21.2	3.7	31	16.3	
1982	Jan	9.8	2.0	25	23.1	3.9	24	16.4	
	Jul	2.8	2.0	25	11.2	2.5	25	7.0	
	A	2.9	2.5	31	13.7	2.8	31	8.3	
	S	3.9	1.6	29	14.1	2.4	30	9.0	
	O	3.9	1.6	29	14.6	3.3	29	9.2	
	N	7.2	2.9	24	21.0	4.2	25	14.1	
	D	7.8	3.0	31	19.5	5.0	31	13.6	
1983	Jan	9.0	3.0	22	22.0	4.0	24	15.5	
	F	9.0	2.0	18	20.0	4.0	20	14.5	
	M	7.6	2.7	31	20.0	4.0	31	13.8	
	A	6.0	2.5	23	17.0	3.6	23	11.5	
	M	5.0	2.7	31	13.0	4.3	31	9.0	
	J	3.0	2.2	31	11.0	2.3	31	7.0	
	J	3.0	2.5	31	9.8	1.9	31	6.4	
	A	3.2	1.9	31	13.1	3.2	31	8.1	
	S	4.6	2.2	30	14.5	2.7	30	9.5	
	O	7.2	3.0	31	15.8	4.1	31	11.5	
	N	8.1	2.3	30	17.4	4.2	30	12.7	
	D	8.1	2.2	31	18.8	3.4	31	13.4	

B.Monthly average temperatures (°C) for all years

J	F	M	A	M	J	J	A	S	O	N	D
16.3	15.6	14.4	12.9	9.3	7.1	7.1	8.4	8.7	10.4	12.9	14.3

C.Rainfall (mm) for months of 1984 and 1985 at Kowhai Bush, Schoolhouse Road (supplied by P Woods, Meteorological Service, Kaikoura)

(i) 1984

Rainfall

J	F	M	A	M	J	J	A	S	O	N	D
–	–	196	130	136	18	131	235	839	54	57	90

Rain days

J	F	M	A	M	J	J	A	S	O	N	D
–	–	13	4	15	3	9	10	11	7	7	6

(ii) 1985

Rainfall

J	F	M	A	M	J	J	A	S	O	N	D
45	72	105	38	–	–	–	–	–	–	–	–

Rain days

J	F	M	A	M	J	J	A	S	O	N	D
6	9	7	10	–	–	–	–	–	–	–	–

APPENDIX 5 : Weather conditions and sampling between seasons and different birds while observing care of young during the nestling period

Weather conditions were scored on each occasion parental care was watched during the nestling periods as described in section two and the general methods. Most of the observations over the nestling periods of nests with and without helpers were made in relatively equable conditions where wind velocity was low, temperature moderate to warm and sunny or partly cloudy days (Table 1).

Table 1 Weather conditions during sampling

A.First clutches

(i) Nonhelper	Scale			
Variable	0	1	2	3
wind	132	53	52	25
temperature	76	130	41	15
cloud cover	67	120	41	34
(ii) Helper				
wind	104	63	27	3
temperature	60	86	45	6
cloud	61	81	30	25

B.Second clutches

(i) Nonhelper				
wind	141	113	51	12
temperature	50	157	84	26
cloud	111	129	42	35
(ii) Helper				
wind	26	10	6	1
temperature	8	23	9	3
cloud	14	17	9	3

B. Observations on nestling parental care:

The total number of occasions nestling parental care was observed were as follows: first clutch non helper - 262, first clutch helper - 197, second clutch non helper - 317, second clutch helper - 43. Each category of nest was observed in the three seasons nestling parental care was studied (Table 2).

Table 2 Occasions nestling parental care was observed each summer

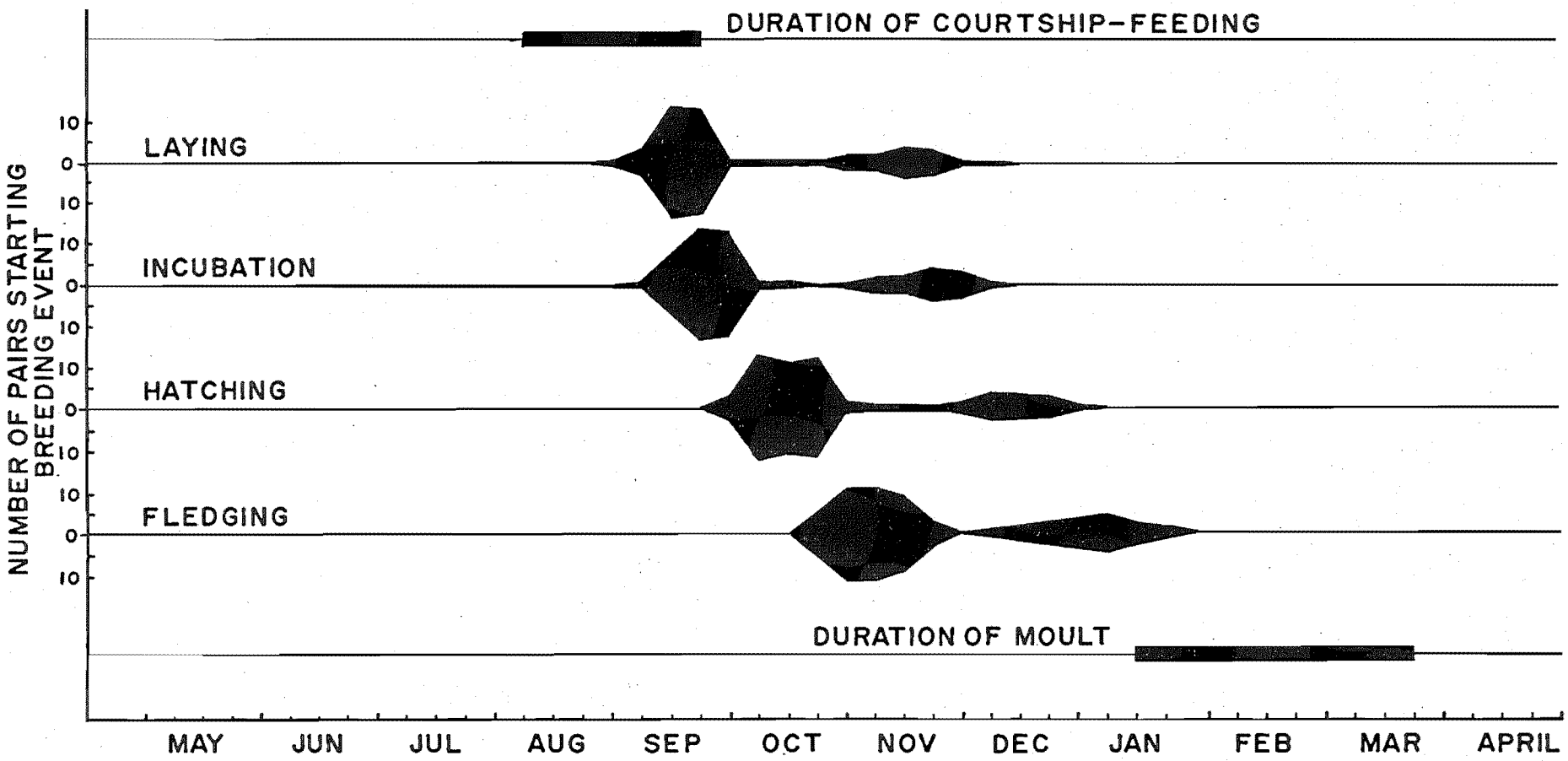
A.First clutch	1980/81	1981/82	1982/83
(i) non helper	19	35	208
(ii) helper	13	164	20
B.Second clutch			
(i) non helper	33	124	160
(ii) helper	0	5	38
Totals	65	378	426

As many different pairs as possible were observed in the day-intervals for each nest category (Table 3).

Table 3 Different pairs and nests watched during nestling parental care

	Day interval						
A.First clutch	1-4	5-8	9-12	13-16	17-20	21-24	Tot
(i) Non helper							
number of nests	14	10	17	17	13	11	25
number of pairs	12	9	17	15	11	9	19
(ii) Helper							
number of nests	-	4	5	4	7	7	9
number of pairs	-	3	4	3	6	6	11
B.Second clutch							
(i) Non helper							
number of nests	11	13	12	11	10	6	15
number of pairs	10	12	11	10	9	6	14
(ii) Helper							
number of nests	-	1	1	1	1	2	2
number of pairs	-	1	1	1	1	2	2

As noted for incubation, the number of different pairs watched is less than the number of nests because some pairs were observed over more than one season.



Appendix 6: The annual cycle of Riflemen

(note: to calculate totals add vertical scale readings each side of zero)